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PIONEER SALIX ALAXENSIS COMMUNITIES ALONG THE
SAGAVANIRKTOK RIVER AND ADJACENT DRAINAGES

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PIONEER *Salix alaxensis* COMMUNITIES ALONG THE SAGAVANIRKTOK RIVER AND ADJACENT DRAINAGES

A

THESIS

Presented to the Faculty of the University of Alaska

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Nancy J. Moore, B.A.

Fairbanks, Alaska

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PIONEER *Salix alaxensis* COMMUNITIES ALONG THE SAGAVANIRKTOK RIVER AND ADJACENT DRAINAGES

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ABSTRACT

This research was part of a larger project concerned with reintroduction of *Salix alaxensis* to sites along the Sagavanirktok River disturbed during construction of the Trans Alaska Oil Pipeline. Objectives were to obtain information on: (1) undisturbed pioneer *Salix alaxensis*-dominated communities; and (2) reproductive potential of *Salix alaxensis*. Individual stands were sampled, mapped, and/or surveyed. Individual plants were sampled for branching patterns, seed production, seed dispersal and germination.

A general pattern of community succession emerges from the community analyses with allogenic factors most important in the youngest communities, and autogenic factors increasingly important as vegetation matures. Succession may be interrupted by fluvial processes at any stage.

Among the most important findings from the population-level studies are that transitional stands were generally the most prolific seed producers; and successful establishment of seedlings appears to depend on the seeds falling on a moist open mineral substrate that remains moist during the summer.

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INTRODUCTION

Gravels required for the construction of the northern section of the Trans Alaska Oil Pipeline were mined primarily from the floodplain and terraces of the Sagavanirktok (Sag) River in arctic Alaska. The mining and construction process resulted in destruction of some riparian willow communities. Agreements between federal regulatory agencies and Alyeska Pipeline Service Company (APSC) stipulated that disturbed critical wildlife habitat would be restored. It was assumed by the agencies that all riparian willow stands qualified as such habitat and APSC was mandated to restore or replace approximately 800 acres of willow stands.

The initial attempt of APSC to plant willows in these areas was unsuccessful. Evaluation of this attempt led to the realization that insufficient knowledge existed to warrant further revegetation efforts without additional information. As a result, APSC contracted with the University of Alaska's School of Agriculture and Land Resources Management for a three-year study investigating techniques for large-scale reintroduction of willows in disturbed areas.

The investigation was separated into three general areas: 1) investigation of techniques for revegetation with willow, specifically *Salix alaxensis*, the primary moose browse species, along the Sag River, 2) characterization of moose habitat and the impact of collection of willow cuttings on willow growth and moose habitat; and 3) investigation of the baseline ecology of naturally occurring *Salix alaxensis* communities along the Sag River.

During the last two years of the study, 1979 and 1980, I conducted research on the third subproject, the investigation of the baseline ecology of *S. alaxensis* communities. The research encompassed two aspects of *S. alaxensis* (feltleaf willow) ecology, analysis of *S. alaxensis* communities and population studies. The community analysis research included collecting information on the species present, percent cover, characteristics of *S. alaxensis* and substrate; the population studies investigated aspects of seed rain, seedling establishment and the reproductive potential of *S. alaxensis* at selected sites.

SITE DESCRIPTION

The Alaskan Arctic is a vast region comprising three basic physiographic provinces, the Brooks Range, the Arctic Foothills and the Coastal Plain (Spetzman 1959, Britton 1966 and Hettinger and Janz 1974). Each province is characterized by unique features of topography, geology, soils, vegetation and variation in climate.

The Arctic is a region of continuous permafrost. Various features resulting from frost-related processes are visible in all provinces; they include solifluction lobes, high and low center polygons, sorted and nonsorted nets, frost boils, beaded streams and thaw lakes and ponds. These features contribute to local variation in topography (Benninghoff 1952 and Britton 1966).

BROOKS RANGE PROVINCE

The southernmost province, the Brooks Range, contains rugged peaks ranging from 900 meters in the west to 3000 meters in the east. The mountains were uplifted during the Cretaceous era and were extensively glaciated during the Pleistocene. Small glaciers persist today on peaks 2000 meters and higher. Exposed rock in these mountains are from the Paleozoic and include Devonian clastics, Mississipian limestone, shale, chert, conglomerate and Permian sandstone (Spetzman 1959 and Payne, et. al. 1951).

Little soil material has accumulated in the mountains due to steep slopes, wind and water erosion, glaciation and frost action. Moraine deposits, alluvial fans and talus slopes are common in mountain valleys (Spetzman 1959).

Numerous vegetation types exist in the Brooks Range; vegetation generally is sparse and varies greatly with microtopography. Species diversity tends to be greater at lower elevations. The most widespread vegetation types are low and dwarf willows and alpine heath and *Dryas* meadows; these types have a variety of species in association with them depending on elevation, aspect, slope and substrate. Lichens are widespread. Taller shrubs, primarily *Salix* spp., are generally confined to stream or lake margins at lower elevations (Britton 1966; Hettinger and Janz 1974; and Viereck and Dyrness 1980).

The mountains are generally cooler than the foothills during the summer and are subject to summer thundershowers; strong winds, through passes and in the valleys, occur throughout the year. Temperature usually decreases with increase in elevation (Spetzman 1959).

FOOTHILLS PROVINCE

This province located north of the Brooks Range is divided into the southern and northern sections. The southern Foothills have a complex and irregular topography often reaching 600-900 meters in elevation. Common features are isolated hills formed from Early Cretaceous, Triassic and Mississipian rocks of sandstone, conglomerate, limestone and chert separated by lowlands underlain by shale. The area has been above sea level since the Early Cretaceous and was not glaciated during the Pleistocene. The northern Foothills are characterized by a more regular topography consisting of east-west ridges, mesas and hills generally 150-600 meters in elevation. Bedrock is mainly composed of shale, conglomerate, sandstone, bentonite or tuff (Spetzman 1959 and Payne, et. al. 1951).

Several rivers originate in the mountains or foothills and flow northward to the Arctic Ocean dissecting the foothills and coastal plain. The Sag River, one of the major arctic rivers, originates in the Phillip Smith Mountains (1500 meters) in the Brooks Range and flows approximately 300km in a northerly direction to the Beaufort Sea immediately east of Prudhoe Bay. *Salix alaxensis* communities along the Sag River were the primary focus of this study.

The Sag River exhibits primarily a split channel configuration in the Foothills region; toward the northern Foothills, the floodplain becomes broader and more braided. In a channel with a split configuration, numerous islands divide the river into two channels. The islands and riverbanks are usually vegetated and stable. The floodplain tends to be narrower and the channels narrower and deeper than in a braided river system (Woodward-Clyde 1980).

At any location the cross section of a river channel is a function of flow, the width of the channel, the quantity and character of the sediment in movement through that section and the composition of the materials making up the bed and banks of the channel (this includes vegetation) (Leopold, et. al. 1964).

In the winter, water stops flowing in many rivers; in those rivers where water continues to flow aufeis may form. Aufeis is ice which forms on top of itself by a series of overflows. (Aufeis was observed along the Sag River in March 1979.) Aufeis and ice jams may increase water levels upstream during spring thaw (Woodward-Clyde 1980).

Peak flow in arctic rivers generally occurs following spring thaw with lesser peaks occurring later in the summer (Gill 1971). During high flow channels scour and, as the water begins to subside, materials are deposited filling to approximately the same level as they were initially by eroding from one bank and depositing on the other bank (Schumm 1977).

Some channels and gravel bars, like portions of the Sag River, contain areas that lack fine particles in the upper strata. Two possible explanations for this occurrence are: (1) the sand and fine gravel are winnowed away by differential water movement, and (2) a sorting process has occurred in which large particles tend to stay on top (Leopold, et. al. 1964).

Fluvial processes are exceedingly complex and not completely understood. However, there is a general feedback process that operates in any channel which interacts between the channel bed and bank characteristics, the flow and the sediment load. This interaction forms the characteristics specific to a certain stretch of river (Leopold, et. al. 1964).

Soils of the orders Entisol, Mollisol and Inceptisol are found in the Arctic Foothills and Coastal Plain Provinces; the Inceptisols are the most extensive soils represented primarily by the Pergelic Cryaquepts subgroup. The Pergelic Cryaquepts are poorly drained, fine-textured soils with varying amounts of organic matter, which overlay permafrost (Rieger, Schoephorster and Furbush 1979). Better drained soils occur on ridges and along river terraces. Alluvial soils containing large amounts of sand and rocks have deep active layers, particularly where there is no plant cover (Spetzman 1959, Britton 1966, and Hettinger 1974).

Since the Foothills Province contains more diverse habitat and better climatic conditions for plant growth, more vegetational diversity is observed than in the Brooks Range or Coastal Plain (Britton 1966). Six broad vegetation types have been identified reflecting variation in soils, drainage and slope. The most extensive types are Wet Sedge Meadows and Tussock Tundra; other types include Dwarf Shrub-Sedge Meadows, Riparian Shrub-Open Forest, Dwarf Heath-Lichen Tundra and Open Dwarf Shrub Heath Barrens. The Riparian Shrub-Open Forest type includes the willow vegetation along streams which sometimes reaches tree size and the balsam poplar stands which grow near springs or underground water sources along the boundary of the Brooks Range and southern Foothills (Hettinger 1974).

Although diurnal and annual temperature ranges are wider in the Foothills Province than on the Coastal Plain or Brooks Range Provinces, the average summer temperatures are warmer. More summer sunshine and slightly more precipitation occur in the Foothills than on the Coast.

Occasional snow flurries occur in summer but temperatures may reach 24°C or greater. Annual precipitation is 10-20cm per year, most occurring in the summer (Spetzman 1959).

Snow does not occur in large amounts yet it can be important; wind-driven snow is abrasive to exposed plant parts. Drifted snow provides protection to plants from wind and melting snow provides a source of water in the spring. Areas of deep snow accumulation which melt slowly shorten the growing season (Britton 1966).

Although the Arctic region is often considered to be arid, Britton (1966) indicates that precipitation exceeds evapo-transpiration during the growing season and additional moisture is available from seasonal melting of ice in the active layer.

COASTAL PLAIN PROVINCE

The Coastal Plain slopes from the Foothills region to sea level; it is divided into two sections, Teshekpuk Lake and White Hills. The Teshekpuk Lake section is the most western and coastal; it is low lying and generally less than 100m above sea level with most of the surface covered by wind-oriented lakes. The White Hills section is easterly and interior to Teshekpuk Lake section, has more topographical variation with elevations rising to 350m or more (Hettinger and Janz 1974).

As recently as the Quaternary period, parts of the Coastal Plain were below sea level (Spetzman 1959). Today thick Quaternary deposits consisting of unconsolidated marine and non-marine gravel, silt, sand, clay and peat occur on most of the plain. However, in the White Hills some non-marine sediments of the Early Tertiary Sagavanirktok Formation of poorly consolidated conglomerates, silty sandstone, siltstone, lignite and cannel coal occur (Payne, et. al. 1951).

As mentioned earlier, the predominant soils are classified as Pergelic Cryaquepts (Rieger, Schoephorster and Furbush 1979).

Vegetation in the Coastal Plain is less diverse than in the Foothills or Brooks Range because there are fewer species and less variation in habitat. However, vegetational associations change with slight variations in microtopography. The major environmental gradient affecting the vegetation is moisture related (Neiland and Hok 1971).

Hettinger and Janz (1974) describe six major vegetation types with Wet Sedge Meadow as the predominant type. Low Shrub Sedge Meadows and Hummocky Tundra and Heath-Sedge Tussock Tundra are frequently encountered. Types accounting for small amounts of cover in the Coastal Plain include Riparian Willow Shrub, Dwarf Shrub-Dryas Meadow and Heath-Sedge Tussock Tundra which occur on slightly better drained sites of alluvial deposits and floodplain terraces.

Diurnal and annual temperatures along the Coast do not have a wide range due to the moderating influence of the Arctic Ocean. Summer temperatures are cool; e.g. average temperature at Barrow for June through August is $4^{o}C$ and winds averaging more then 20km per hour persist throughout the summer. Seventy percent of the time there is fog or cloud cover (Spetzman 1959).

Investigation of the baseline ecology of S. *alaxensis* (feltleaf willow) was conducted in riparian willow communities along the Sag River in the Foothills Province. Intensive study sites were located along a 45km stretch of river, from 2km south of Pump Station 3 of the Trans Alaska Oil Pipeline northward to the former Happy Valley construction camp (Figure 1). Because the study sites occurred along the pipeline corridor, they were given names that corresponded to nearby material sites, construction camps or pump stations. The names are consistent with those used during the construction of the Trans Alaska Oil Pipeline and the period shortly after the pipeline was completed.

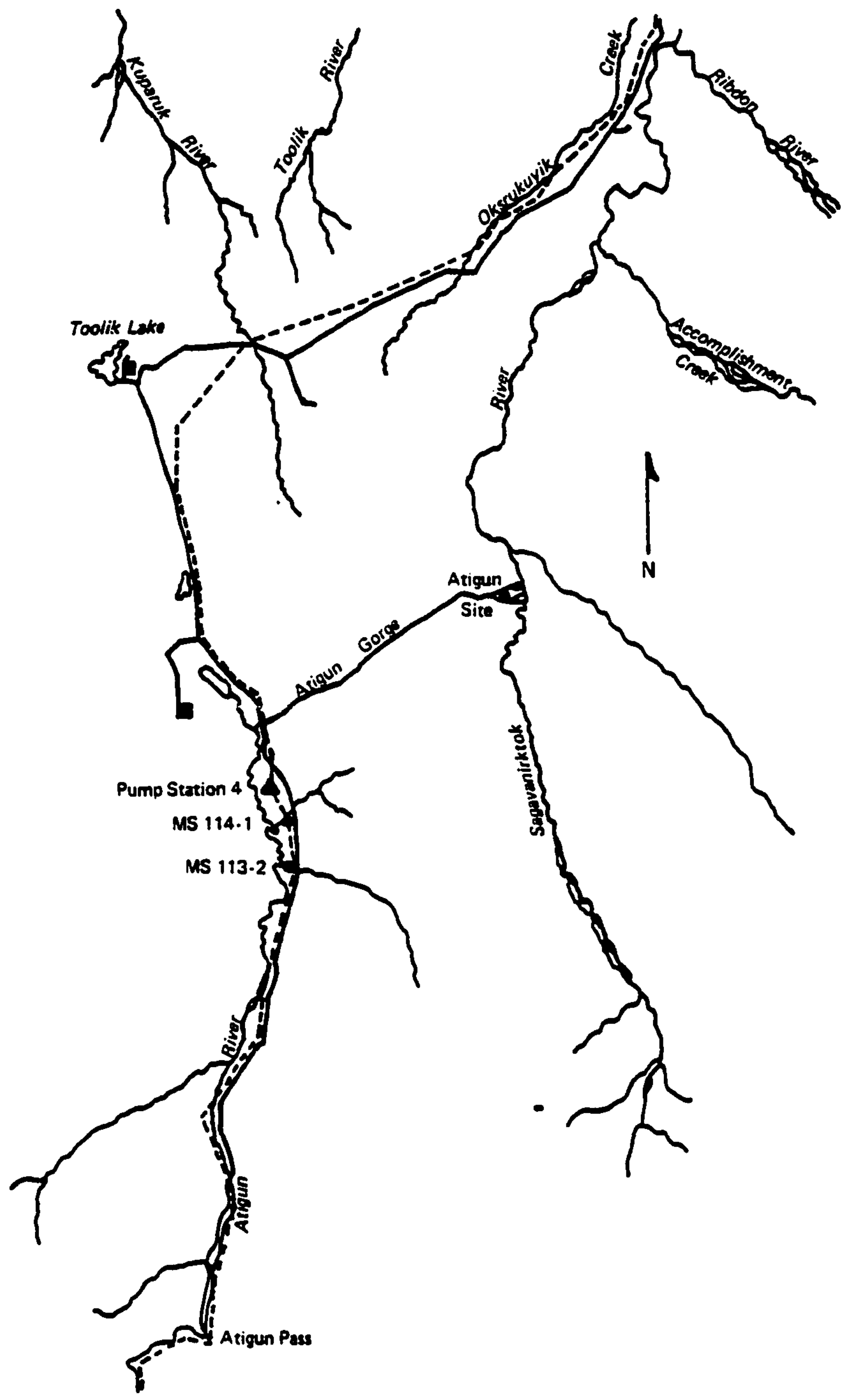

Figure 1a. Map of study areas (southern half)

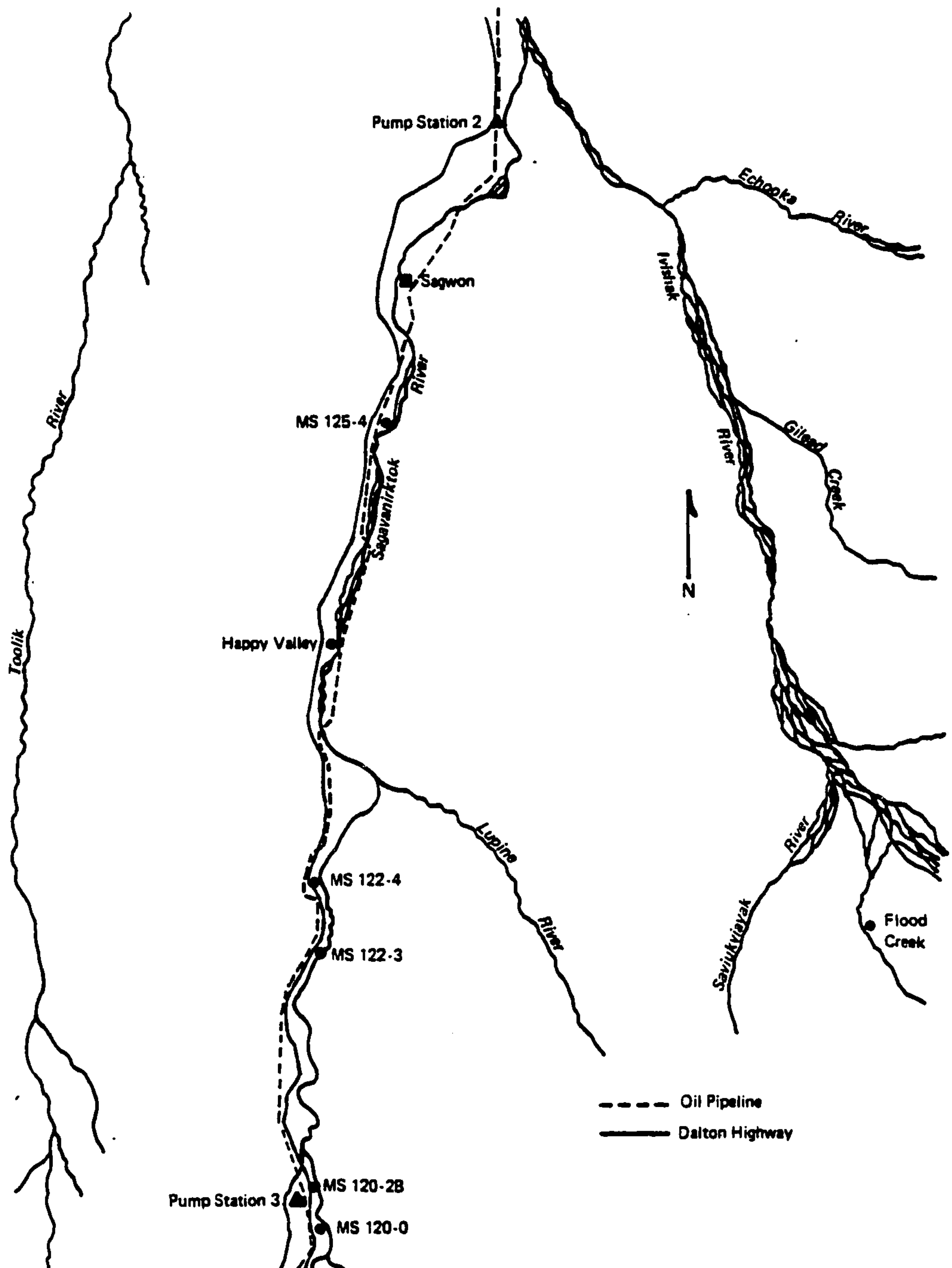

Figure 1b. Map of study areas (northern half)

LITERATURE REVIEW

Numerous authors have described the colonization of newly emerged river alluvium in Alaska and Northwestern Canada (Drury 1956; Bliss and Cantlon 1957; Spetzman 1959; Wiggins and Thomas 1962; Britton 1966; Johnson, Viereck, et. al. 1966; Johnson and Vogel 1966; Gill 1971; Viereck 1970; Argus 1973; Hettinger and Janz 1974; Young 1974; and Neiland and Viereck 1977). Although some variation is noted in the floristics of the early successional communities, particularly between the forested and non-forested regions, similar broad successional patterns and associated environmental changes occur.

During the pioneer successional stages physical factors are more important than biotic factors for plant colonization. Physical factors include character of substrate gravel, sand or silt; frequency and duration of flooding; erosion and deposition. As ground cover increases, additional sedimentation by finer textured material occurs, flooding and associated impacts are reduced and biotic factors become increasingly more important for plant development. Increasing amounts of leaf litter, vegetative mat and finer soil particles provide an insulating blanket which decreases soil temperatures, influences soil chemistry and drainage and eventually allows the development of permafrost (Drury 1956, Bliss and Cantlon 1957, Spetzman 1959, Gill 1971, and Viereck 1971).

Soil temperatures recorded at 50cm depths in a young gravel bar feltleaf willow stand and an adjacent decadent stand along the

Sagavanirktok (Sag) River showed that soils were warmer in the young stand by 5-6^{o}C in June and 2^{o}C in July. Temperatures were the same in August (Neiland and Zasada 1980).

The nutrient status of river alluvium has been described as moderate (Bliss and Cantlon 1957, and McLeod and McPherson 1972) to hydroponic by Nechaev (1967). Soil samples collected from some arctic Alaskan drainages indicate that low nutrient levels exist, particularly for nitrogen and phosphorous at Flood Creek and the Sag River. These drainages which originate in limestone mountains, exhibit high pH levels which negatively influence nutrient availability. Soils from other drainages originating in the foothills had lower soil pH values, 5.5-6, which is in the range where mineral nutrients are more readily available (Neiland and Zasada 1980).

Discussion of the development of vegetation in the floodplain of the Bureya River by Nechaev (1967) emphasizes the importance of edaphic conditions over climate. Microtopographical variation resulting from river dynamics strongly influences the pattern of plant colonization. The composition of alluvium determines drainage, depths of dry layers, depth to water table and temperature regime. The lower areas of gravel bars tend to have finer alluvial particles than the elevated areas; they also have reduced temperature fluctuations, no or shallow dry layers and are subject to flooding by small fluctuations in water level. Some members of the genus *Salix* are capable of colonizing these low gravel areas.

The earliest pioneer community described by Gill (1971) originated on silt alluvium along active channels of the MacKenzie River Delta and consisted of *Equisetum fluvatile* and a few other herbs. On higher ground slightly further removed from the river, the next successional stage included *Salix alaxensis* and *Equisetum* spp. Poplar seedlings were also found in this community. As *S. alaxensis* matures and becomes senescent, poplar overtops the shrub layer and dominates the next successional stage. An important herb of this stage is the legume, *Hedysarum alpinum*, which, in association with a nitrogen fixing bacterium increases the nitrogen content of the nitrogen-poor alluvium (Gill 1972). Subsequent stages include decadent poplar followed by a white spruce dominated community.

Similar patterns are described for forested regions of Alaska, the Chena River and Kuskokwin River in interior Alaska, but additional successional stages following white spruce include mixed white and black spruce and black spruce-*Sphagnum* communities (Neiland and Viereck 1977, Viereck 1970, and Drury 1956).

Other successional sequences described by Gill (1971) develop on stable and static channels; the plants are less vigorous than those in the sequence observed on the active channel. The static channel sequence also begins with *Equisetum fluvatile* followed by *Equisetum* spp. and *Salix alaxensis*. The third stage is described as a steady state *Salix* community containing six species of willow and diverse herbaceous taxa. Older *S. alaxensis* shrubs share dominance with *S. richardsonii* and *S. arbusculoides*. Further succession may occur to mixed *Salix*-*Alnus* or white spruce communities.

The stable channel pattern occurs where an equilibrium between erosion and deposition appears to be established, hence changes in physical factors are minimized. *Carex aquatilis* colonizes the margin of the stable channel with few associated taxa; this stage is followed by a limited occurrence of a *Salix-Carex* community including *S. alaxensis* and *S. planifolia* spp. *pulchra*. Further successional development from the *Salix-Carex* community may include *Salix-Alnus*, *Salix* or *Populus* communities.

Succession on river alluvium of the treeless regions of the arctic has also been described (Bliss and Cantlon 1957, Spetzman 1959, Britton 1966, Johnson and Viereck 1966, Argus 1973, and Hettinger and Janz 1974). In this region, different species of willow are often the dominant vegetation in various successional stages instead of the tree vegetation found in forested regions.

Four broad riparian communities identified by Bliss and Cantlon (1957) were perennial herb, young feltleaf willow, decadent feltleaf willow and the higher terrace communities which include low shrub, marsh, heath and tussock meadow vegetation types. Herbs including *Crepis nana*, *Epilobium latifolium*, *Artemisia* spp., *Oxytropis* sp., *Astragalus alpinus*, *Lupinus arcticus*, and the shrub *S. alaxensis* are the primary pioneer species of the perennial herb community. Other willows include *S. arbusculoides* and *S. glauca*. Pioneer species become established on silt and sand pockets in the gravel alluvium. Vegetation is sparse but locally can be quite dense particularly in association with *S. alaxensis* shrubs. The subsequent stage, the young feltleaf willow community, contains tall *S. alaxensis* shrubs often attaining several meters in height. Where shrub growth is dense, the understory is sparse. Additional shrubs include *S. glauca*, *Salix hastata*, *S. arbusculoides*, *S. lanata* and *Alnus crispa*. As *S. alaxensis* shrub vigor declines and dead stems become more prevalent in the decadent feltleaf willow community, other *Salix* species become more important. These species include *S. arbusculoides* and *S. glauca; S. hastata* is absent and *S. brachycarpa* is observed for the first time. In the relatively higher undisturbed terrace communities, a variety of vegetation types can occur. In the shrubby types, the dominant shrub generally is *S. planifolia* spp. *pulchra* in association with *S. lanata* spp. *richardsonii*, *S. glauca* and *S. arbusculoides* (Bliss and Cantlon 1957, Spetzman 1959, and Argus 1973).

Other variations in the successional pattern just described have been noted by Johnson and Viereck (1966), Argus (1973) and Hettinger and Janz (1974). Along Ogotoruk Creek during early successional stages, the two most important willows are *S. planifolia* spp. *pulchra* and *S. alaxensis*, the latter being more important nearer the coast. Shrubs nearer the coast are generally shorter than those found inland in the foothills region. In later successional stages on infrequently flooded terraces, *S. planifolia* spp. *pulchra* is the dominant willow (Johnson and Viereck 1966). Argus (1973) emphasizes the change in *Salix* composition and growth form from the gravel floodplain to upper terraces for a creek near Cape Beaufort. Taller willows, .5m and greater, including *S. alaxensis*, occur on the floodplain while dwarf species, less than 3dm tall, occur on relatively stable upper terraces primarily on well-drained sites. Hettinger and Janz (1974) note that *S. alaxensis* is more important in Alaska than in the Yukon where *S. glauca* and *S. planifolia* spp. *pulchra* usually occur in riparian succession.

Johnson and Vogel (1966) describe the age structure of subarctic *Salix* vegetation on the Yukon as progressing from 9 to 41 years with distance from the active river channel. Viereck (1970) notes that along the Chena River that within 10 to 15 years of initial colonization of gravel bar, balsam poplar is able to overtop feltleaf willow. Neiland and Viereck (1977) note that the willow-alder shrub stage usually lasts for 15 to 25 years on the interior floodplains while in some areas such as the Porcupine River and Yukon Flats floodplain, the shrub stage is longer.

General age of arctic riparian willow communities is described for early successional stages (20-30 years). At this time, feltleaf willow and numerous herbs are most prevalent. By 45-50 years, feltleaf willow is no longer the dominant shrub, being replaced by *S. planifolia* spp. *pulchra*, *S. lanata* spp. *richardsonii* and *S. glauca* (Hettinger and Janz 1974). Bliss and Cantlon (1957) agree with this successional time frame. They note that *S. alaxensis* stems in their decadent feltleaf willow community (*S. alaxensis* is still dominant but several other willows have become more important) had up to 46 'annual' rings. Given that riparian willows can experience repeated burials by river alluvium and send up new sprouts (Gill 1971), the question arises of how well do ages of willow stems reflect the true age of individual shrubs or of the stand.

Characteristics of *S. alaxensis* that contribute to its success as a pioneer riparian shrub include: It is one of the most sun-tolerant willows; it disperses large amounts of seed early in the summer; the seed having no dormancy requirements can germinate on newly exposed substrate after the floodwaters from spring thaw subside (Nechaev 1967, Gill 1971, and Argus 1973); *S. alaxensis* develops adventitious roots readily (Zasada and Densmore 1978), an important trait in habitats in which burial of branches is apt to occur. Growth of sprouts from buried branches often produces dense stands of feltleaf willow (Viereck 1970, and Johnson and Vogel 1966).

Salix alaxensis seed is extremely shortlived; one compensation for the seed's short life appears to be its ability to germinate over a wide range of soil temperatures (Zasada and Viereck 1975).

A moist substrate is very important for germination and seedling establishment of the riparian species of *Salix*. The *Salix* seed rapidly produces hypocotyl hairs after landing on a moist substrate; these hairs attach the seed to the substrate and absorb water and minerals for the expanding root and cotyledons. Since the root develops slowly, hypocotyl hairs need to be able to function for approximately one week on a moist substrate for the seedling to survive (McLeod and McPherson 1972). In addition, the cotyledons begin photosynthesizing before shedding the seed coat (Nechaev 1967). Both of these traits may help compensate for small seed size.

Many species of willows are capable of maintaining root function under limited oxygen availability and are highly tolerant of flooding (McLeod and McPherson 1972).

In their work on black willow (*Salix nigra*), McLeod and McPherson (1972) note that established plants have a much broader ecological range than do their seedlings. Factors limiting the distribution of black willow are related to moisture availability for seedling establishment. Seed dispersal needs to coincide with the prolonged availability of a moist substrate while the slow growing root reaches a more reliable water supply than surface moisture. The narrow moisture range of seedlings seems to be characteristic of feltleaf willow also.

Asexual reproduction is often considered to be the most common form of reproduction in the arctic. This may be true for tundra areas of shallowly thawed soils where few seedlings are observed; however, seedlings are quite common on deeply thawed soils as found in the floodplains (Bliss 1958).

Billings (1974) discusses three requirements for establishment of seedlings in the arctic: 1) a seedling needs enough time to develop a root system and to produce enough carbohydrates to allow survival through the following winter; 2) summer temperatures need to be warm enough for good germination and growth; and 3) adequate moisture needs to be present until seedlings can reach a reliable water supply. A fourth requirement, as noted above, is that seed dispersal needs to coincide closely with the availability of a favorable substrate since seed viability is very short (Nechaev 1967).

Invasion of the gravel bars by *S. alaxensis* has been described as occurring both asexually and sexually. Bliss and Cantlon (1957) describe clumps of *S. alaxensis* shrubs being deposited on gravel bars after having been eroded from cutbanks upstream. They also observed a few seedlings. Studies by Woodward-Clyde Consultants (1980) also describe seed and vegetative origins of invading *S. alaxensis* shrubs for mined areas in river floodplains. The source of some of the vegetative material came from overburden distributed over the disturbed area. Neiland (personal communication) observed what appeared to be time sequences from newly deposited clumps of *S. alaxensis* to clumps deposited by earlier floods along Ogotoruk Creek. The latter range from obviously dead and eroding root-branch masses to clumps with new roots penetrating well into the gravel and vigorous new shoots. Invasion of river alluvium by seed appears to be the most common means of colonization by *S. alaxensis* in the MacKenzie Delta (Gill 1971).

Salix alaxensis is found in arctic, alpine and boreal areas on gravel bars and terraces of rivers, streams and lakes and in alpine meadows. It ranges throughout Alaska except for most of the Aleutian Islands, some Bering Sea islands and southeastern Alaska south of Glacier Bay. *Salix alaxensis* is also found in the Yukon Territory, British Columbia and the Canadian Arctic. It ranges south in the Rocky Mountains to Jasper National Park and is found in parts of Asia (Argus 1973).

Two varieties of *S. alaxensis*, var. *alaxensis* and var. *longistylis*, are recognized by Argus (1973). The var. *longistylis* tends to be less pubescent, have smaller buds, and grow taller and more treelike than the var. *alaxensis*. Characteristics of the two varieties often intergrade and are highly variable in themselves making the reliable distinction between the two varieties often difficult. One of the main arguments for recognition of these taxa is var. *alaxensis* occurs more frequently in the Arctic and at higher elevations than var. *longistylis*.

COMMUNITY LEVEL STUDIES

METHODS

1979 Methods

In 1979 several areas were investigated along the Sag River and other drainages in an attempt to broaden information on the variability to be found in young *Salix alaxensis* communities. The three Sag River sites were adjacent to Material Sites 120-2B, 122-3 and Happy Valley runway; sites located in other drainages were Oks Creek, a Sag River tributary, Material Site 113-2 located on an alluvial fan in the northern Brooks Range, Flood Creek, Kuparuk River and the mouth of the Atigun River (Figure 1). Only a short time was spent at the latter three sites which were accessible only by helicopter and data collected from these sites were limited.

Four broad community types, designated low gravel, high gravel, transition and mature were identified to assist in describing the vegetation. The community types, representing points along a continuum of generalized vegetation development, were differentiated on the basis of size and growth form of *S. alaxensis*, the proportion of *S. alaxensis* to other willow species, amount and type of associated herbs, and substrate. Rationale for the determination of community types follows in the discussion of General Community Types.

Stands representative of the low gravel, high gravel and transition community types were sampled. Twenty one-meter square plots were systematically placed in each selected stand in order to uniformly distribute the plots throughout the stand.

Information collected from each plot included species presence, number of individuals, percent cover, height of the tallest ramet[1] for each willow genet[1] providing cover in the plot and substrate data, which included the percent of gravel versus silt and sand and the size of gravel in the plot. Although a mixture of gravel and rock sizes occurred within the plots, gravel size was noted as the largest rock diameter found in a given plot.

The nomenclature utilized in this text follows The Genus *Salix* for Alaska and the Yukon (Argus 1973) for willows and Flora of Alaska and Neighboring Territories (Hultén 1974) for other vascular plants.

1980 Methods

Methods for 1980 were modified from those used in 1979 so that more information could be gathered on the dynamic process of vegetation development at riparian sites.

Three Sag River sites containing riparian *S. alaxensis* dominated communities were selected for study. Stands of different communities

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[1]A ramet is an emergent stem of an individual shrub or genet. A genet can be comprised of one or several ramets, but it is considered to be a single individual.

within each site were mapped and stands representative of the range of variation at each site were selected for sampling.

The criteria for site selection were: minimal disturbance by construction activities; partially sampled in 1979; contained different communities; and reasonably accessible by road and foot. It was possible to map and sample three such sites during the summer of 1980.

Use of aerial photographs facilitated the delineation of the study area and mapping process. Different communities within the study area were identified on the aerial photographs and their boundaries were verified on the ground.

Plot sampling techniques utilized in 1979 were repeated in 1980. Data presented in the Results and Discussion section are from 1980. Instances where 1979 data differ from 1980 data will be noted.

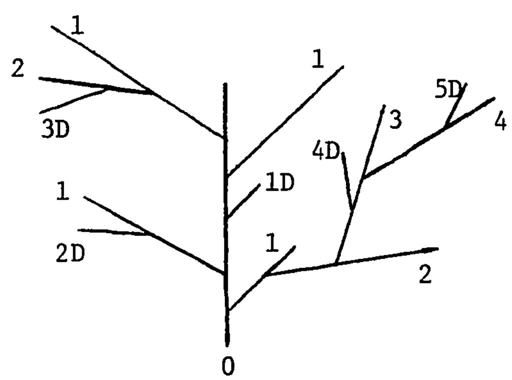
At least one stand representing each of the four general community types, i.e., low gravel, high gravel, transition and mature, was sampled at site 122-3; at site 120-0 all types except the low gravel type were sampled and at the Happy Valley site, all types except the transition type were sampled.

The feltleaf willow communities that were not selected for intensive sampling were qualitatively described. A species list, substrate data and general observations were obtained for each of these communities.

From each of the intensively sampled communities, additional data on shrub growth and structure were collected. *Salix alaxensis* ramets were harvested along transects which extended the length of the community. Harvest occurred from August 6 to 11 at which time leaf senescence and abscission had begun. Depending upon the density of feltleaf willow, every ramet, every other ramet, or every third ramet was selected for harvest. No more than three ramets were harvested from one genet. The basal diameter (outside the bark) of each ramet was measured with vernier calipers. The ramets were air dried for four to five weeks after which all leaves, dehiscent twigs and dead wood were removed and the ramet was weighed on a triple beam balance to the nearest .01 gram. The branch order of the longest current season's growth was also noted. The smallest ramets were weighed later at the University of Alaska on a Mettler balance to the nearest milligram.

The total ramet collection was divided into subsamples on the basis of stem diameter. The live wood of five ramets representing each of the four size classes, 1, 1-2, 2-3 and 3-4 centimeters, was oven dried for 48 hours at 65°C, cooled to room temperature and then weighed on a triple beam balance. The difference between the oven-dry weight and the air-dry weight of these ramets was averaged for each size class to obtain an average oven-dry correction factor. The correction factor was applied to all of the air-dry weights for the ramets occurring in each size class. Age was determined for each ramet by annual ring counts of a basal stem section. To facilitate age determination, each section was sanded until the surface was smooth and then stained using the following procedure: one minute in a solution of one percent phloroglucinol in 95 percent ethyl alcohol followed by immersion in a 36 percent solution of hydrochloric acid for one minute or until adequate staining occurred. The section was then rinsed and air dried. This dye stains lignin red and does not affect cellulose. However, sometimes all of the wood became stained, but partial-to-complete staining made counting rings easier than if the wood was left unstained. Staining was especially helpful in aging the rotted wood that often occurred in S. *alaxensis* stems.

The ramets collected from site 120-0 were also analyzed for branching pattern. The number of living branches that occurred in a particular order was recorded. The zero order was assigned to the portion of stem for which basal diameter and age were measured. A branch originating from the main stem (0 order) was designated a first order branch and a branch originating from a first order was designated as a second order branch, etc. (see below).



D = dehiscent

Numbers 1, 2, 3, etc., represent the order of branching.

Although growth is sympodial in S. *alaxensis*, the shoot that carried on the apical growth continued to be designated the zero order branch. If a branch split into two branches and it was impossible to determine which, if either, of the two branches developed first, then both the branches were designated the next order of branching.

Dehiscent branches were found on the *S. alaxensis* ramets and their branch order was recorded separately from that of the non-dehiscent branches. Branches were considered to be dehiscent if one or more of the following criteria were met: an abscission zone had formed at the base of the branch, the branch was less vigorous than a non-dehiscent branch of the current season, or the branch was less than 10 centimeters in length and buds were absent or poorly developed.

RESULTS AND DISCUSSION

General Community Types

Introduction

Plant communities are complex and composed of species each of which has its own unique distribution patterns. Different communities often intergrade from one to another making the establishment of community boundaries an arbitrary process. A researcher initially investigating a landscape informally organizes plant communities based on what is perceived to be most important. Eventually it may become helpful to develop a more formalized concept of community type based on early field observations. A standardized approach to defining community types such as the Braun-Blanquet system may be utilized allowing data to be comparable to that of other studies or a non-standardized approach which is specifically suited for a particular study may be most useful. In either case, characteristics are selected which define the community type; these characteristics will determine the boundaries of a particular community and influence the type of information gathered (Whittaker 1978).

A non-standard definition of a community type was used in this study. Four broad community types were defined to facilitate the generalized description of the process of change in *Salix alaxensis* dominated vegetation; they are low gravel, high gravel, transition and mature community types. Characteristics of the four community types were listed in the Methods section and will be discussed more completely in the following descriptions of each of the types.

Although most stands fit into one of the community types, some stands were not easily classified because they combined traits of two or more types or had traits not easily attributable to any of the four types. These stands were not classified but are described in the appropriate place along with discussions of specific sites. The following discussions of the four community types are based on combined values for all stands of each type sampled in 1979 and 1980 by twenty one-meter square plots.

Low Gravel Community Type

The low gravel community type is characterized by frequent flooding, little vegetation and a gravel substrate containing few fine particles. The effects of flooding are probably most severe during spring thaw when the movement of ice is added to the movement of gravel. Probably during most spring floods, water volume is greater and the period of flooding of longer duration than during summer floods. Spring flooding creates new seedbeds and impacts vegetation established in previous years. Plants can be eroded to varying degrees or have new gravel material deposited on top of them. Summer flooding and associated weather patterns can also influence patterns of flowering, seed development, seed dispersal, seedling germination, seedling establishment and photosynthesis; the latter three are the most important factors influencing the development of low gravel vegetation.

Often the first impression of a low gravel community is that no vegetation is present (Figure 2). Closer inspection reveals a few small plants growing scattered throughout the community. *Epilobium latifolium* was one taxon which seemed to be clustered probably because of its ability to reproduce vegetatively. Most plants were small with few leaves. *Salix alaxensis* occurred as seedlings with cotyledons and one to three small true leaves, or as small saplings generally less that 25 centimeters tall. Grasses had two or three leaf blades; mosses occurred as small fragments beside rocks and other species were represented by seedlings or very small plants.

The low gravel communities are in the earliest stages of vegetational succession. Eleven percent of the ground surface was covered by vegetation, the two most important species being *S. alaxensis* and *Epilobium latifolium* (Table 1). A total of 28 taxa were found in the community type. Some taxa such as *Arctostaphylos alpina, Salix reticulata* and *Potentilla* sp. were part of the vegetation mats eroded from upriver sites and left stranded on the gravel bar when high water receded. Other taxa most commonly observed in the low gravel communities were grasses, *Aster sibiricus, Equisetum variegatum, Hedysarum Mackenzii, Astragalus* or *Oxytropis* spp., *Stellaria* sp., *Crepis nana* and mosses. Three *Salix* species other than *S. alaxensis* were present;

Figure 2. Low gravel community type at Flood Creek.

Figure 3. High gravel community type at site 122-3.

Table 1. Average of percent cover for species in each community type[1].

Taxa[2]/Community Type	Low Gravel	High Gravel	Transition	Mature
Salix alaxensis	1	5	17	30
S. glauca-brachycarpa[3]	+[4]	+	+	7
S. hastata	+	+	+	8
S. lanata	+	+	+	+
S. arbusculoides		+	+	
Shepherdia canadensis			+	4
Rosa acicularis		+		
No. of seedlings (1979/1980)				
Salix alaxensis	300/150	10/425	1210/650	
Salix spp.	5/0			–/50
Arctostaphylos alpina	+		+	10
S. reticulata	+	+		
Vaccinium uglinosium			+	+
S. arctica			+	
Rhododenron lapponicum		+		
Epilobium latifolium	1	4	1	+
Gramineae	+	+	1	3
Hedysarum Macenzii	+	3	5	3
H. alpinum	+	+	1	9
Astcr sibiricus	+	+	+	3
Polygonum viviparum	+	+	+	+
Astragalus/Oxytropis spp.[5]	+	+	2	
Artemisia spp.	+	1		+
Melandrium spp.	+	+	+	
Senecio spp.		+	+	2
Oxytropis campestris		+	+	1
Lupinus arcticus		+	+	1
Castilleja caudata		+	+	+
Oxytropis deflexa		+	+	+
Pedicularis spp.		+	+	+

Table 1. Continued.

Taxa/Community Type	Low Gravel	High Gravel	Transition	Mature
Potentilla sp.	+		+	
Juncus sp.	+		+	
Astragalus aboriginum		+		+
Oxytropis borealis		+		+
Carex sp.		+		
Papver sp.		+		
Oxytropis Maydelliana		+		
Zygadenas elegans				+
Petasites sp.				+
Astragalus alpinum	+	+	+	2
Equisetum variegatum	+	+	+	+
Stellaria sp.	+	+	+	+
Equisetum spp.	+	+	+	+
Crepis nana	+	+	+	
Carophyllaceae	+	+	+	
Parnassia spp.	+		+	+
Carex spp.		+	+	+
Dryas integrifolia		+	+	+
Unknown herb	+		+	
Gentiana spp.			+	+
Astragalus eucosmus			+	+
Dryas drummondii	+			
Galium sp.			+	
Anemone parviflora				4
Pinguicula sp.				+
Pyrola asarifolia				+

Table 1. Continued.

Taxa/Community Type	Low Gravel	High Gravel	Transition	Mature
Moss	+	1	5	17
Algae	+		+	+
Liverworts	+		+	+
Lichens		+	+	+
Unknown			+	+
Total vascular plant spp's groups (1 group gramineae)	25	35	38	37
Total taxa	28	37	43	42
Total cover 3 + 's = 1%	11	25	42	113

[1]Values for each community type include 1979 and 1980 data and are calculated only for those stands containing 20 plots. Various number of stands were available for each community type calculation: Low Gravels, 9 stands; High Gravel, 10 stands; Transition, 7 stands; and Mature, 3 stands.

[2]Taxa are grouped according to like form: Tall shrubs, seedlings of tall shrubs, low growing shrubs, tall herbs, low growing herbs, and non-vascular plants.

[3]*Salix glauca* and *S. brachycarpa* are closely related species, similar in appearance. Both species may be found in riparian sites but *S. glauca* will also occur in upland tundra. Some shrubs are easily identified as one species and others are intermediate in appearance. Most of the shrubs in the *S. glauca-brachycarpa* complex are *S. glauca* (Neiland and Zasada, 1981).

[4]The "+" indicates the percent cover was less than 1.

[5]This taxa was utilized during 1979, presumably most of the species found in this taxa are represented by those identified more specifically in 1980.

Salix glauca-brachycarpa, S. hastata and *S. lanata*. *Salix* seedlings were also noted with the highest numbers occurring in 1979; they were predominantly *S. alaxensis* seedlings. More detailed discussion of the characteristics of the *S. alaxensis* found in specific stands will be found in the following sections describing communities at each of the study sites and in the section on Population Studies.

The substrate of the low gravel communities consists primarily of gravel. The surface of nearly 90 percent of the plots sampled in the low gravel communities had gravel cover of 75 percent or more. Of the gravel, 80 percent was 20-40 centimeters in diameter (Tables 2 and 3).

High Gravel Community Type

The high gravel community type experiences less disturbance and generally is located on higher terraces than the low gravel community (Figure 3). Vegetation cover is sparse, but fairly conspicuous; *Salix alaxensis, Epilobium latifolium* and legumes, particularly *Hedysarum Mackenzii*, are the most important taxa. Distributions of plants in this community type varied with different stands; the pattern probably reflects the conditions present when the seeds germinated and the plants became established as well as results of disturbances and general history of the stand since colonization. The plants are generally evenly distributed, with most species, including *S. alaxensis* and *Hedysarum Mackenzii*, usually less than 30-40 centimeters in height.

Other differences in the high gravel type compared to low gravel

Table 2. Summary of largest gravel size found in plots for each community type, 1980
Values are percent of plots in each size category.

	Gravel Size (centimeters)				
Community Type	0-10	⩽20	⩽30	⩽40	>40
Low Gravel	0	10	60	20	10
High Gravel	4	18	42	23	13
Transition	45	32	15	8	0
Mature	98	2	0	0	0

Table 3. Percent gravel in plots per community type, 1980
Values are percent of plots in each size category.

	Percent Gravel					
Community	0[1]	⩽25	⩽50	⩽75	⩽90	⩽100
Low Gravel	0	0	5	8	22	65
High Gravel	4	2	4	21	28	41
Transition	24	25	13	7	13	18
Mature	98	2	0	0	0	0

[1] This surface consisted primarily of silt and sand.

type include: taller *S. alaxensis* (Table 4), and greater total cover by all species, especially by *S. alaxensis* and *Epilobium latifolium*. An increase in species diversity is also seen in the high gravel type. *Salix arbusculoides* was noted for the first time; it was part of a vegetative mat also containing *Rosa acicularis*. *Rhododendron lapponicum* and *S. reticulata* were also part of vegetative mats left by high water.

New herbaceous species include several legumes, *Castilleja caudata*, *Senecio* spp., *Pedicularis* spp., *Carex* spp. and *Dryas integrifolia*. Lichens were observed in one stand but are more commonly found in the older and less disturbed stands characteristic of the transition and mature community types. Although *S. alaxensis* seedlings were also observed, they occurred primarily in one stand and were considerably more numerous in 1980 than 1979.

The substrate of the high gravel community type is predominantly gravel. In Tables 2 and 3, trends toward smaller gravel sizes and decreasing amounts of gravel and increasing amounts of silt and sand can be seen progressing from the low to the high gravel types.

Transition Community Type

The transition community type generally is higher and a greater distance from the main river channel and subject to less frequent and probably less severe disturbances than the two previously discussed community types. It usually is quite open (Figure 4) although total

Table 4. Heights of *Salix alaxensis* by community type

Community type	S.a.[1]	Percentage of S. alaxensis per size class (meters) ≤.25	≤.5	≤.75	≤1.0	≤1.5	≥1.5
Low Gravel	49	97[2]	3	0	0	0	0
High Gravel	212	66	33	1	0	0	0
Transition	68	15	15	19	31	16	4
Mature	83	1	11	11	35	31	11

[1] Total number of *S. alaxensis* in all stands of community type sampled.

[2] Percent of total number of *S. alaxensis* individual heights for all stands sampled within type.

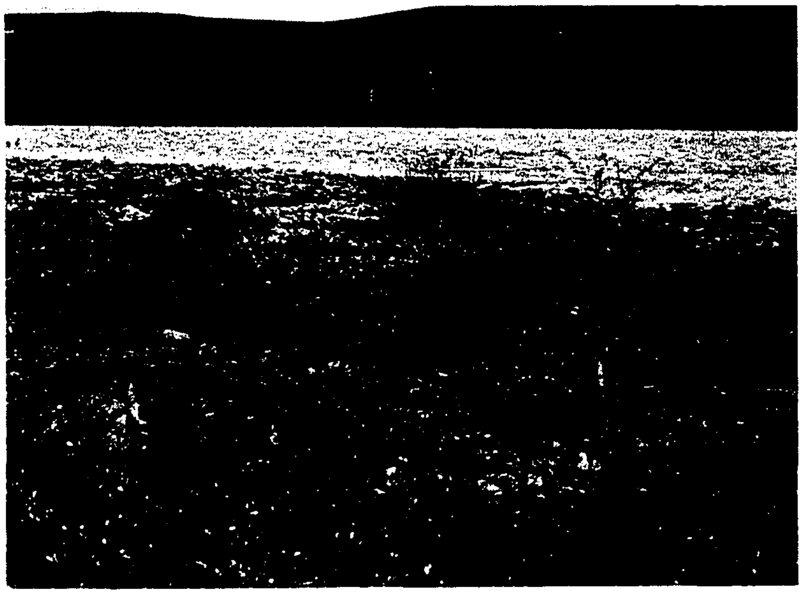


Figure 4. Transition community type at site 122-3.

Figure 5. Mature community type at site 120-0. Much taller shrubs are found in some mature stands. Note the large amount of herbaceous vegetation (center foreground).

plant cover is greater than that of the high gravel community (total cover is 42 and 25 percent, respectively). *Salix alaxensis* contributes nearly half of the transition community's cover. Shrubs found in this community type generally are tall, vigorous with little or no dead wood, well developed and often prolific catkin and seed producers. Further discussion of seed production relative to community types will be found in the section on Reproductive Potential.

Compared with the high gravel type, diversity of herbaceous species is only slightly higher in the transition type (Table 1); however, species composition differs somewhat. Willow species other than *S. alaxensis* are present and cover values were similar to those found in the high gravel type. *Hedysarum Mackenzii* is one of the more important herbaceous species in the transition type as in the high gravel type. New taxa observed in the transition community type included the shrubs *Sheperdia canadensis*, *Vaccinium* sp., and *S. arctica*, and the smaller herbs *Parnassia* spp. and *Gentiana* sp.

The substrate of the transition community differs from that in the high gravel community type in containing smaller size gravel and larger areas with little or no gravel (Tables 2 and 3). The character of the substrate also suggests that this community type experiences less severe disturbance by flooding. Smaller gravel, silt and sand are more likely to be carried into and deposited in areas of slow water flow.

Mature Community Type

The mature community type generally experiences the least disturbance by flooding of the four community types. Inundation probably only occurs during the most extreme high water conditions, which are most often associated with spring thaw.

The appearance of the mature community type differs from other community types because of the high total plant cover, the increase in diversity and the presence of two well-developed strata, the herbaceous stratum and the shrub stratum (Figure 5). The mature type also contains taller *S. alaxensis* than observed in other community types, but the shrubs generally appear less vigorous and contain more dead wood. Cover values for *S. alaxensis* were greater than the cover values in the transition type, but cover values for two other willows, *S. glauca-brachycarpa* and *S. hastata* are much greater (an increase of 57, 700 and 800 percent, respectively).

Other plant groups that showed large cover values in the mature community type compared to the transition community type included the prostrate shrub *Arctostaphylos alpina*, the rank herbs, *Hedysarum alpinum*, *Aster sibiricus*, *Senecio* spp., and the non-vascular plant group, the mosses. *Anemone parviflora*, rarely observed in stands representing other community types, appears in the mature community type as one of the more important herbs (Table 1).

The substrate of the mature community type contained 98 percent sand and silt. Small amounts of gravel were present, with diameters generally less than 10 centimeters. The character of the substrate like the vegetation suggests that less disturbance occurs in the mature community type than in the other types. Flood water with a high silt and sand load and slowed by vegetation probably produces a substrate such as that found in the mature community type. Silt and sand deposits were observed on the downstream side of the larger shrubs.

Sag River Intensive Study Sites

Introduction

Three intensive study sites were selected along the Sag River in 1980. The most southern site is approximately 2km south of Pump Station 3 near the access road to Material Site 120-0 and is referred to as Site 120-0. Farther north, and down river, Site 122-3 is located toward the river from Material Site 122-3. The most northern site, Happy Valley, is located east of the runway that once served the now inactive Happy Valley Camp.

Although all three sites are riparian sites, they differ geomorphologically. The willow communities at Site 120-0 occur around a side channel of the Sag River, while those at 122-3 have developed on a point bar. At Happy Valley, the communities have developed around a gravel bar that is building along its northern and southern sides while eroding along a portion of the north-eastern edge of the gravel bar.

The substrate of the younger willow communities was primarily gravel with some silt and sand patches. Two exceptions include the transition stand of 122-3 and the north central portion of the young willow communities at Happy Valley in which the substrate was primarily silt and sand. Other differences between sites include: Site 120-0 had no low gravel community large enough to sample, unlike the other two sites, and Happy Valley successional patterns were patchier than those at the other two sites. Despite the physical differences, vegetational similarities exist among the three sites.

Comparison of the quantitative data reveals some of the similarities in the community types (Tables 5a and 5b). Approximately 70 percent of the species recorded at each of the sites were species common to all the sites. *Salix alaxensis* was the principal tall shrub at all sites and its cover value exceeded cover values for all other species in each of the community types at each of the sites, with one exception. In the high gravel community at Happy Valley, the cover values for *Hedysarum Mackenzii* and *S. alaxensis* were equal. Intermediate shrub species included *S. hastata* and *S. glauca-brachycarpa*. These two willows occurred in the high gravel, transition and mature communities of Sites 122-3 and Happy Valley; at 120-0 they occurred only in the transition and mature communities. *Salix glauca-brachycarpa* and *S. hastata* had their highest cover values in the mature communities at all three sites. Another intermediate shrub present in the mature community at all sites was *Shepherdia canadensis*.

The number of willow seedlings observed seemed to be very low and was probably influenced by the differences in sites, community types, substrates and timing of visits to the study areas. *Salix alaxensis* seedlings were observed in all community types except the mature type, and were most frequent at 122-3. Additional discussions of seedling establishment and seed production will be found in the sections on Reproductive Potential and Seedling Dynamics.

Table 5a. Percent cover of plant species occurring on foodplain sites along the Sag River, 1980

	Percent cover/square meter based on 20-1m² plots														
	120-0						122-3					Happy Valley			
	high gravel		transition		mature stand		low gravel	high gravel		transition	mature	low gravel	high gravel	mature stand	
	Q	W	M	J	F	L	A	B	H	C	E	A	B	D	S
Salix alaxensis	3	4	20	28	44	10	+	1	7	11	20	1	11	25	10
S. glauca-brachycarpa				+	5			+	+	+	6		+	9	1
S. hastata					4			+	+	+	9		+	11	2
Shepherdia canadensis				2	3						4			4	
S. lanata													+	+	+
S. arbusculoides			1												
Total No. of seedlings															
S. alaxensis			25					75	350	625		150			150
Salix spp.											25			25	
Arctostaphlyos alpina				+	6						7			17	+
Vacinnium uliginosium										+	+			+	+
S. arctica										+					
S. reticulata														+	
Gramineae	+	+	+	+	3	+	+	+	1	1	4	+	+	3	5
Epilobium latifolium	1	1	3		+	1	1	1	4	+	1	1	6	+	1
Hedysarum Mackenzii		+	11	12	5	+		1	+	+	4		11	+	+
Aster sibiricus					2		+	+	+	+	4	+	+	4	+
Hedysarum alpinum		+	2	1	8			+	+	+	5		+	6	
Castilleja caudata			+		+			+	+	+	+		+	+	+
Senecio spp.		+	+		2				+		2		+	3	+
Oxytropis campestris			2	2	4				+		+		+	+	
Lupinus arcticus			2	1	3	+							1	+	
Polygonum viviparum					1			+		+				+	+
Astragalus aboriginum								+	+				+	+	
Oxytropis deflexa		+	+	+											
Oxytropis borealis					1				+						
Artemisia spp.		+			+								+		
Juncus sp.										+					1
Carex sp.		+													
Oxytropis Maydelliana													+		
Petasites sp.											+				
Pedicularis sp.														+	
Zyadenas elegans														+	
Eriophorum sp.															+

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Table 5a. Continued.

	Percent cover/square meter based on 20-1 m^2 plots														
	120-0						122-3					Happy Valley			
	high gravel		transition		mature stand		low gravel	high gravel		transition	mature	low gravel	high gravel	mature stand	
	Q	W	M	J	F	L	A	B	H	C	E	A	B	D	S
Equisetum variegatum	+	+	+		+		+	+	+	1	+	+	+	+	5
Astragalus alpinus		+	1	2	5	+	+	+	+	+	+		+	+	
Stellaria sp.					+				+	+	+	+		+	+
Crepis nana								+	+	+		+	+		
Carex spp.					1					+	+			1	2
Equisetum spp.		+								+	+			+	2
Parnassia sp.										+	+			+	1
Gentiana sp.					+					+				+	+
Anemone parviflora					+						+			1	+
Astragalus eucosmus					1					+					
Pyrola asarifolia					1						+				
Dryas integrifolia											+				
Pinquicula sp.														+	
Carophyllaceae															+
Tofielda sp.															+
Moss			1	2	11	+	+	+	+	+	19	+	2	20	9
Lichens				+	+						+			+	
Liverwort											+			+	1
Unknown					+									+	+
Algae											+				
Total vascular spp./group	4	12	13	11	25	6	6	14	17	22	24	7	19	30	24
Total spp./group	4	12	14	13	28	7	7	15	18	23	28	8	20	34	27
Total cover – % 3 +'s = 1%	4	9	45	51	113	13	3	7	17	20	90	4	36	111	45

Table 5b. Percent frequency of species occurring on floodplain sites along the Sag River.

	Percent frequency/square meter based on 20-1 m^2 plots														
	120-0						122-3					Happy Valley			
	high gravel		transition		mature	stand	low gravel	high gravel		transition	mature	low gravel	high gravel	mature	stand
	Q	W	M	J	F	L	A	B	H	C	E	A	B	D	S
Salix alexensis	35	80	50	100	90	60	55	45	95	55	90	50	100	90	100
S. glauca-brachycarpa				10	50			5	5	15	90		5	80	55
S. hastata					30			10	30	10	50		5	70	100
Sherpherdia canadensis				10	30						25			5	
Salix lanata													5	5	15
S. arbusculoides			5												
Seedlings															
S. alaxensis			5					15	95	40		45			5
Salix											5			5	
Arctostaphylos alpina				5	25						25			80	10
Vacinnium uliginosium										5	5			10	5
S. arctica										5					
S. reticulata														5	
Gramineae	5	20	15	10	60	5	15	45	70	65	80	45	25	95	95
Epilobium latifolium	45	80	65		5	20	75	80	85	35	15	30	60	10	35
Hedysarum Mackenzii		20	80	65	75	10		50	15	20	70		80	15	20
Aster sibiricus					55		10	5	10	30	85	10	15	95	25
Hedysarum alpinum		5	30	20	60			5	10	15	75		25	80	
Castilleja caudata			5		25			5	5	15	30		10	30	10
Senecio spp.		5	10		65				10		70		5	85	40
Oxytropis campestris			45	40	55				5		20		5	10	
Lupinus arcticus			25	10	70	10							5	5	
Polygonum viviparum					15			5		10				5	20
Astragalus aboriginum								10	10				5	5	
Oxytropis deflexa		5	5	10											
O. borealis					15				5						
Artemisia spp.		5			5								25		
Jancus sp.										30					85
Carex sp.		10													
Oxytropis Maydelliana													5		
Petasites sp.											5				
Pedicularis sp.														15	
Zyadenas elegans														5	
Eriophorum sp.															30

continued on next page

Table 5b. Continued.

	Percent frequency/square meter based on 20-1 m² plots														
	120-0						122-3					Happy Valley			
	high gravel		transition		mature stand		low gravel	high gravel		transition	mature	low gravel	high gravel	mature stand	
	Q	W	M	J	F	L	A	B	H	C	E	A	B	D	S
Equisetum variegatum	5	35	10	10			5	35	70	65	55	40	5	50	95
Astragalus alpinus		5	30	45	70	5	5	10	10	5	20		10	5	
Stellaria sp.					60				15	10	40	5		60	10
Crepis nana								20	5	10		5	5		
Carex spp.					20					5	30			55	80
Equisetum spp.		5								40	15			15	80
Parnassia sp.										5	5			50	70
Gentiana sp.					5					5				50	15
Anemone parviflora					5						15			30	5
Astragalus eucosmus					50					5					
Pyrola asarifolia					5						15				
Dryas integrifolia											5				
Pinquicula sp.														5	
Carophyllaceae															5
Tofielda sp.															5
Moss			60	85	95	5	5	5	45	35	100	40	75	100	100
Lichens				10	5						35			10	
Liverwort											15			5	50
Unknown					70									5	25
Algae										5					

Arctostaphylos alpina was the most important prostrate shrub, the highest cover values occurred in the mature community. Other prostrate shrubs whose presence was rare included *Vaccinium ulginosum, Salix reticulata* and *S. arctica*.

The tall herbs exhibited similar patterns in the three study areas. Grasses, although they did not contribute a large amount of cover, were found in all stands; they were more vigorous and more diverse in the mature stands. *Epilobium latifolium* was found in all community types but not all stands; it was absent in one transition stand at 120-0. The greatest cover values for *Epilobium latifolium* occurred in the high gravel stands or open transition stands. *Hedysarum Mackenzii* and *H. alpinum* occurred in all stands except the two low gravel stands. However, the relative importance of the two species changed in the different community types. Generally, *H. Mackenzii* was more important than *H. alpinum* in the high gravel and transition stands; the reverse was true for the mature stands. *Polygonum viviparum* had low cover values but occurred in all mature stands sampled. Other herbs in this plant group appeared to occur with no particular pattern and their presence was rare. Tables 5a and 5b indicate that the taller herbs including *Aster sibiricus, Castilleja caudata, Senecio* spp., *Oxytropis campestris,* and *Lupinus arcticus* are fairly common; presence of these species varies with community and site. Three of the most apparent differences are the absence of *Aster sibiricus* from all but the mature stand at 120-0, the diversity and relatively high cover values for legumes at 120-0 compared to the other sites and the total absence of *Lupinus arcticus* from site 122-3.

The low growing herbs generally have low cover values in these willow communities. *Equisetum variegatum* and *Astragalus alpinus* are the most widespread and were found in at least one stand of each community type at each site. Other low herbs the sites had in common were generally found in the mature community type. They included *Stellaria* sp., *Equisetum* spp., *Carex* spp., *Parnassia* spp., *Anemone parviflora* and *Gentiana* spp.

Of the non-vascular species, mosses were widespread and were found to some extent in each of the community types. At all sites the importance of the mosses was lower in the low gravel and high gravel stands and higher in the mature stands. Other non-vascular taxa included lichens and liverworts, which also were observed primarily in mature stands. These latter taxa contributed little cover to the community and were relatively rare in these riparian communities.

Site 120-0

Introduction

The *Salix alaxensis* communities of 120-0, the southernmost site, are oriented primarily around a side channel (Figures 6 and 7). The side channels were areas that were being colonized naturally and periodically inundated. During high water, the side channel began to fill with water from the northern end into Stand W. The water

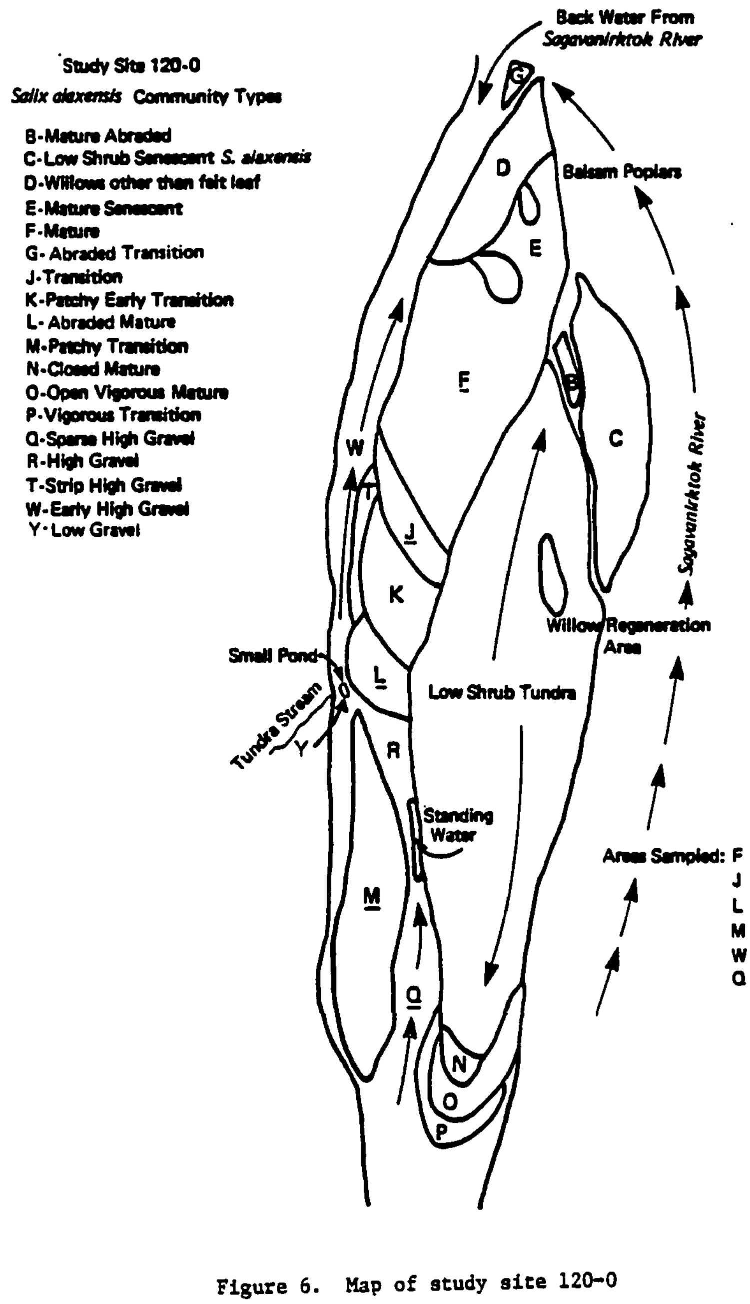

Figure 6. Map of study site 120-0

Figure 7. Aerial photograph of site 120-0 (1980). Note marks on the gravel channel from the lower left, up and towards center left through stand Q (Figure 6). These marks were probably made by rocks and ice carried by spring runoff.

movement in this area at the early stages of flooding appeared to be gentle, causing minimal erosion; disturbances to the vegetation probably were limited to the interruption of normal physiological processes. Since water movement was slow and the river's silt load appeared to be heavier during flood conditions, deposits of silt might occur. A thin coating of silt was observed on rocks on the northern end of the channel after high water had subsided. The silt, if deposited on leaves, could interfere with photosynthesis.

When water levels became high enough, surface water flowed from the upstream or southern end of the side channel, flowing first into the narrow channel furthest from the river. The pond on the wider channel north of Stand Q increased in volume. Water came from precipitation, ground water or both. Ground water was observed coming to the surface near Stand W and also at the other two sites.

When water levels became very high, water flowed in the channel marked Stand Q. Aerial photographs revealed scour lines parallel to the river channel; these were most apparent at the southern end of Stand Q. Additional evidence of abrasion by flood waters occurred along both edges and at the southern end of Stand M, where willow stems had been stripped of bark and bent over. The most dramatic example of abrasion occurred in Stand L where shrubs had been severely damaged. Areas that did not appear to be subject to flooding included the low shrub tundra and communities C and D. These areas were slightly higher than the surrounding communities.

During non-flood periods, surface water was limited to two ponds, one at the north end of Stand Q and the other at the south end of Stand W. The latter small pond was fed in part by a small tundra stream that flowed into the side channel (Figure 6). The stream flowed over a small gravel area that supported a dense cluster of young willows. Whether or not the stream or the ponds persisted all summer is unknown, but they were present during seed dispersal. Also unknown is the extent of the fluctuation of the water table and subsurface water movement.

High Gravel Stands

Stand Q

The physical descriptors outlined for high gravel communities in the discussion of community types generally apply to Stand Q; vegetation was very sparse and there were indications that severe disturbance occurred at the southern end of the stand (Figure 7). Plant cover was least at the southern end and slightly greater toward the northern end of the stand. More severe disturbance at the southern end and the presence of a small pond at the northern end of the stand might have contributed to the observed differences in plant cover.

With respect to low total plant cover and low diversity (Table 5a), Stand Q resembled a low gravel community; however, the growth form of *S. alaxensis* and physical characteristics of the stand were more compatible with the definition of the high gravel community type. Only four taxa were recorded in the stand, *S. alaxensis* (the primary cover), grasses, *Epilobium latifolium* and *Equisetum variegatum*. The most widely distributed taxa, *S. alaxensis* and *Epilobium latifolium*, were the only taxa occurring in more than one plot and they were recorded less than 50 percent of the time (Table 5b). Two other willows, *S. glauca-brachycarpa* and *S. hastata* were also present in the stand, but were not recorded in the plots.

Each of the four taxa recorded in the plot are capable of surviving disturbances which might be important for colonization of this area. *Salix alaxensis* shrubs have long stout root systems and the ability to root adventitiously, *Epilobium latifolium* and *Equisetum variegatum* have rhizomes and the grasses have rhizomes and subsurface buds.

Only eight *S. alaxensis* shrubs occurred within the plot sample, and most were approximately 30 centimeters tall (Table 6). The mean age of the 21 ramets was six years and the ramets ranged from one to 12 years (Figure 8). The shrubs also showed signs of erosion (Figure 9), i.e., a portion of the root had been exposed, but no stem abrasion was noted.

Stand W

Stand W was lower in elevation than Stand Q and although it was apparently inundated more frequently than Q, the disturbance did not seem to be as severe. Scrape marks on the substrate surface were absent, but some willows were partially eroded and had exposed roots.

Stand W appeared to be more moist than Stand Q, possibly due to a

Table 6. Summary of heights of willows found in plots at 120-0, 1980
Values are percent of shrubs in each size category.

Community Type	Total No. of Shrubs	Shrub Height (meters) ≤.25	≤.50	≤.75	≤1.0	≤1.5	>1.5
		Percent Shrubs/Height Category					
S. alaxensis							
High Gravel Q	8	25	75	0	0	0	0
High Gravel W	39	85	15	0	0	0	0
Transition M	14	7	7	7	29	29	21
Transition J	37	11	2	30	76	11	0
Mature F	24	0	4	4	25	46	21
Stand L[1]	16	25	43	13	6	13	0
S. hastata[2]							
Mature F	9	22	22	45	0	11	0
S. glauca brachycarpa							
Transition J	2	50	0	50	0	0	0
Mature F	21	19	33	29	14	5	0
S. arbusculoides							
Transition M	1	0	0	0	100	0	0

[1]The height categories for this community more appropriately refer to length since shrubs have been bent to the ground.

[2]Only stands containing *Salix* spp. other than *S. Alaxensis* are listed.

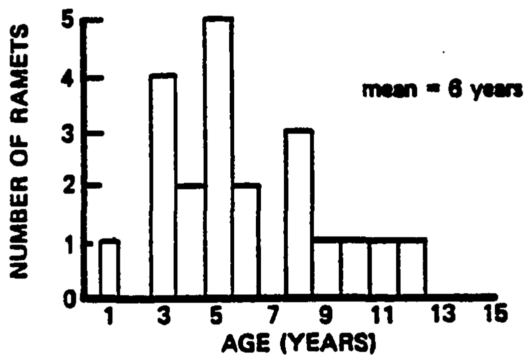

Figure 8. Age transect data from high gravel stand Q, site 120-0. The sample consisted of 21 ramets collected from 21 genets.

Figure 9. Young willow with root partially exposed, stand W, site 120-0.

higher water table, and the small stream and pond that existed at the southern edge of the community. Comparison of the data from Stands W and Q show that the former contained three times as many species as the latter (Table 5a). The cover values for *S. alaxensis*, grasses, *Epilobium latifolium* and *Equisetum variegatum* were the same for the two stands; however, *S. alaxensis* and *Epilobium latifolium* were the most widely distributed taxa. *Equisetum variegatum*, grasses, *Hedysarum Mackenzii* and the remaining taxa, were found in one or two plots. Stand W contained the following taxa not found in Stand Q: *Hedysarum Mackenzii, H. alpinum, Oxytropis deflexa, Astragalus alpinus, Senecio* spp., *Artemisia* spp., and *Carex* sp. The presence of *Carex* sp. suggests a moist substrate.

The *S. alaxensis* found in Stand W seemed to differ from those in Stand Q; they tended to be shorter but slightly older (Table 6 and Figure 10). Approximately five times as many *S. alaxensis* shrubs occurred in the plots in Stand W than in Stand Q yet the cover values are similar. The substrate of Stand W contains large gravel and very little sand and tends to be coarser and more moist than that found in Stand Q (Tables 7 and 8).

Transition Stands

Stand M

The transition community M was an island of open vegetation between two side channels of the Sag River (Figure 6). Consistent

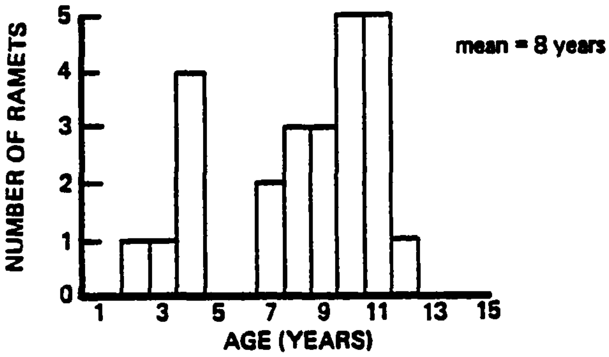

Figure 10. Age transect data from high gravel stand W, site 120-0. The sample consisted of 25 ramets collected from 24 genets.

Table 7. Summary of largest gravel size found in plots at 120-0, 1980
Values are percent of plots in each size category.

	Gravel Size (centimeters)				
Stand	0-10	<20	<30	<40	>40
High Gravel Q.	5	10	45	30	10
High Gravel W.	0	15	25	30	30
Transition M	10	35	35	20	0
Transition J	40	45	10	5	0
Mature F	95	1	0	0	0
Stand L	0	25	50	25	0

Table 8. Summary of percent gravel in plots per community type at 120-0, 1980
Values are percent of plots in each size category.

	Percent Gravel					
Stand	0	<25	<50	<75	<90	>100
High Gravel Q.	5	5	5	15	15	55
High Gravel W.	0	0	0	5	15	80
Transition M	0	30	20	5	20	25
Transition J	0	20	15	15	20	30
Mature F	95	5	0	0	0	0
Stand L	0	5	5	5	0	85

with the general description for transition communities, this area appeared to be infrequently disturbed. The gravel, silt and sand ratios and gravel size were slightly larger than those found in the general description. Willows on the southern end and eastern edges of the stand, which were slightly lower than the rest of the stand show signs of disturbance; they were abraded and bent down to varying degrees.

The vegetation had a patchy distribution. Willows tended to be clustered with two to four shrubs together and their growth form was full, well developed and tall (Table 6). Herbs were often associated with the willows but the legumes, particularly *Hedysarum Mackenzii* and *Lupinus arcticus*, often occurred in the open areas. Taxa more widely distributed than *S. alaxensis* were *H. Mackenzii*, *Epilobium latifolium* and the mosses (Table 5b).

Total cover in Stand M was greater than in the high gravel Stands W and Q (Table 5a); *S. alaxensis* and *Hedysarum Mackenzii* were the two most important species in the stand with cover values of 20 and 11 percent, respectively. Other species in Stand M had cover values of three percent or less. Comparison of taxa diversity revealed no important differences between transition Stand M and high gravel Stand W.

Salix alaxensis ramets collected from the stand gave an age distribution of 3 to 28 years (Figure 11). Since more than one ramet was collected from several of the genets, the age distribution data might suggest that the community was slightly younger than it actually

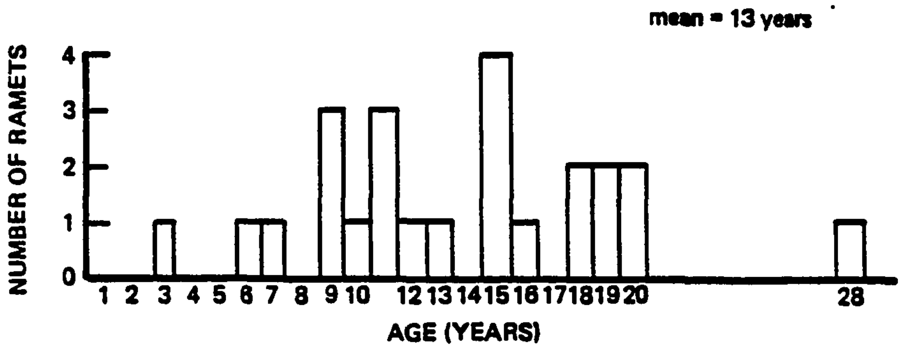

Figure 11. Age transect data from transition stand M, site 120-0. The sample consisted of 25 ramets collected from 14 genets.

appeared; the mean age was 13.

The substrate was gravel, silt and sand; the gravel-silt-sand ratios and gravel sizes were slightly larger than those of the general transition community type (Tables 7 and 8). These coarse substrates seemed like excellent solar collectors and because of the mass they would also retain heat well (Mazria 1979). Warm soils might be an important factor contributing to the vigor of the willows found in this stand.

Stand J

The transition community J was located between two other communities; K, a transition stand, and F, a mature stand (Figure 6). Stand J occupied an elevated terrace where disturbance by flooding appeared to be infrequent.

Stand J differed from the transition Stand M in several ways (Figures 12 and 13), including: substrate, vegetation and S. *alaxensis* growth form and age.

The size of gravel in Stand J tended to be smaller than that in Stand M but the ratio of gravel to silt and sand was similar. The substrate in Stand J appeared compacted, the relatively uniformly sized gravel seemed pressed into a matrix of sand and silt which supported some moss. This compact substrate did not occur in Stand M.

Vegetation differences between Stands M and J existed but were minimal, except for those related to S. *alaxensis*. In the intermediate shrub category, Stand J contained S. *glauca-brachycarpa* and *Shepherdia canadensis*, chiefly at the eastern end of the stand. (Density of

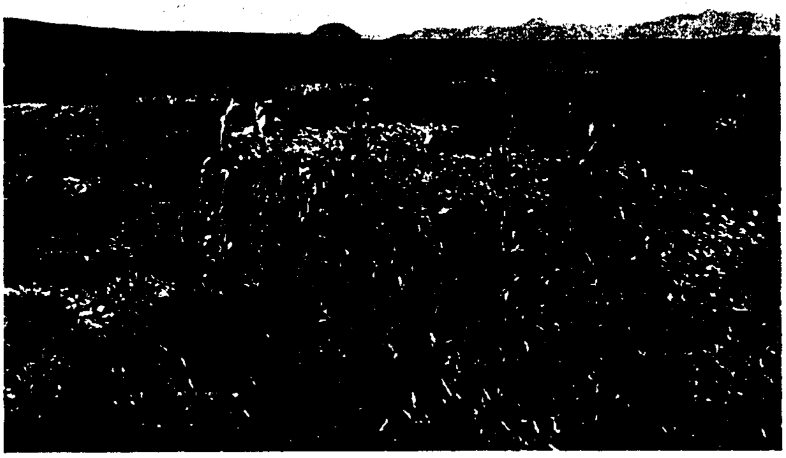

Figure 12. Transition stand M: Note patchy distribution of *Salix alaxensis* and large open gravel spaces.

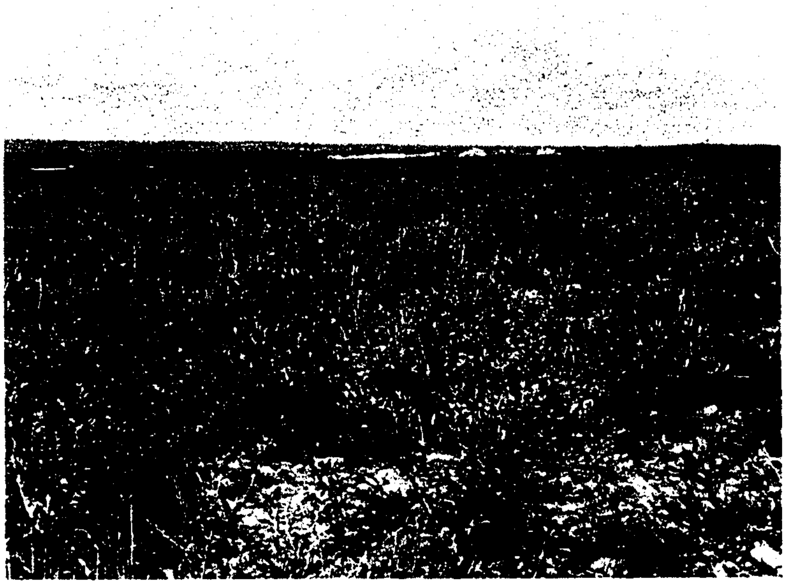

Figure 13. Transition stand J: Shrubs are more uniform in size and distribution than those found in stand M.

shrubs other than *S. alaxensis* was higher on the eastern edge, adjacent to shrub tundra, in communities J, K and F) (Figure 6). The prostrate shrub *Arctostaphylos alpina* also occurred in Stand J. None of these shrub species were found in Stand M.

Compared with those of Stand M, *S. alaxensis* shrubs in Stand J were generally more uniform in height, shorter, less vigorous and had a more uniform distribution (Tables 5b and 6). The average ages of the ramets from Stand J were higher than those of Stand M (16 and 13, respectively) while the range was slightly less for Stand J (6-25 and 3-28, respectively) (Figure 14).

In the tall herb group, *Epilobium latifolium, Castilleja caudata, Senecio* spp. and *Oxytropis deflexa* were found in the plots in Stand M but not in J, although all but *Oxytropis deflexa* occurred outside the sampled area in Stand J. *Equisetum variegatum* occurred only in Stand M and lichens only in Stand J. The occurrence of lichens and the three shrubs in Stand J but not Stand M suggests that less disturbance occurs in the former.

Mature Stand F

The mature community F was located north of and adjacent to the transition community J. The substrate of stand F was primarily silt, sand and small gravel (Tables 7 and 8). The stand, bordered on three sides by other shrub communities, was most vulnerable to disturbance along the western edge where the side channel occurs; however, it appeared to be infrequently disturbed. Along the eastern edge of the

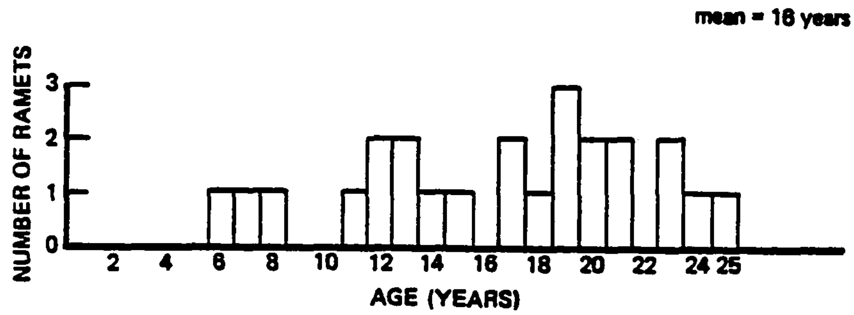

Figure 14. Age transect data from transition stand J, site 120-0. The sample consisted of 25 ramets collected from 20 genets.

stand, next to the low shrub tundra, there appeared to be an old narrow side channel which might fill with water or snow and influence stand dynamics.

Stand F had substantial within-stand variation. Two basic patterns were observed, one parallel to the river and the other more or less perpendicular to the river. The pattern parallel to the river was characterized by increasing vigor of *S. alaxensis* and decreasing herbaceous cover proceeding south in the stand. The pattern perpendicular to the main river channel was characterized by decreasing vigor of *S. alaxensis* and increasing density of *S. glauca-brachycarpa*, *S. hastata* and *Shepherdia canadensis* toward the eastern edge of the stand and the border with shrub tundra. Stand F had twice the total cover and greater diversity of taxa than either transition Stand J or M; higher cover values were found for *S. alaxensis*, *S. glauca-brachycarpa* and *S. hastata* and the latter two shrubs occurred more frequently than in other stands (Tables 5a and 5b). These willows were also taller in Stand F than in other sampled stands (Table 6). Ninety percent of the *S. alaxensis* were taller than .75 meters and most *S. glauca-brachycarpa* and *S. hastata* shrubs were .5 meters tall or taller. Ramets of *S. alaxensis* collected in this stand were older than ramets collected from the other community types discussed thus far; the range of ages was 10 to 35 years, and the mean was 22 years (Figure 15).

Other taxa for which higher cover values and frequency were recorded were *Arctostaphylos alpina*, Gramineae, *Hedysarum alpinum*,

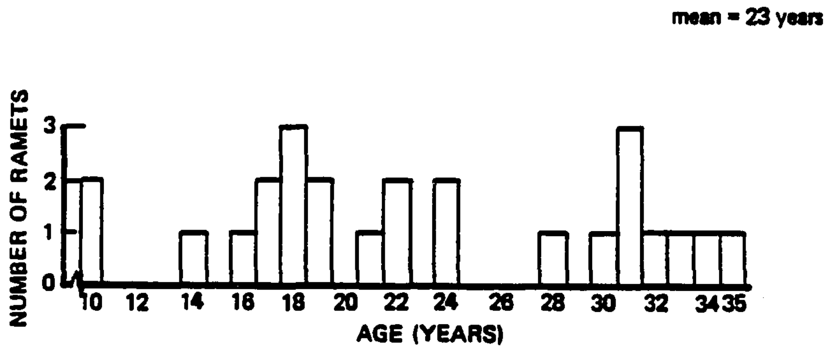

Figure 15. Age transect data from mature stand F, site 120-0. The sample consisted of 21 ramets collected from 25 genets.

Senecio spp., *Oxytropis campestris*, *Lupinus arcticus*, *Astragalus alpinus*, and mosses. Contributing to the total herbaceous cover but recorded only in the mature community at 120-0 were: *Aster sibiricus*, *Polygonum viviparum*, *Oxytropis borealis*, *Stellaria* sp., *Carex* spp., *Anemone parviflora*, *Gentiana* spp., *Pyrola asarifolia* and *Astragalus eucosmus*. Cover values were lower for *Epilobium latifolium* and *Hedysarum Mackenzii* than in the transition stands.

Other Stands

Numerous *S. alaxensis* communities existed at 120-0 other than those discussed earlier (Figure 6). One of these communities was sampled quantitatively; others were qualitatively described. However, many of these communities did not differ greatly from those mentioned in the earlier discussion, but some differed substantially and are discussed below.

Stand L

One of the sampled areas at study site 120-0 did not readily fit into the four basic community types. Community L was unusual in that it contained what appeared to be old shrubs that had been severely damaged by floods. The substrate was predominantly gravel, 10-40 centimeters in diameter and the associated vegetation was sparse.

The stand was located at the confluence of the two side channels of the Sag River. The elevation increased from Stand R to Stand K (Figure 6). During spring floods it appeared that turbulent water movement carrying ice and large gravel occurred in these side channels.

The movement of these substances probably forced *S. alaxensis* shrubs over, eroding some while partially burying others. Early in the spring, the shrubs appeared dead; all had stems that were severely abraded, the bark was partially stripped and some wood was shredded (Figures 16 and 17). Later in the summer, these shrubs produced some of the most vigorous growth observed in any of the stands from buds on the protected portions of the stem (Figures 18 and 19). Despite the vigorous growth, total *S. alaxensis* cover was low at 10 percent. Cover of *S. alaxensis* was half of that found in Stand M, although the shubs in Stand L had a slightly wider distribution than those of Stand M (Tables 5a and 5b).

There were few shrubs in the stand, which led to modification of the technique for collecting ramets. As mentioned in the Methods Section, each ramet, rather than every other or every third ramet in Stand L, was collected for age analysis. This technique yielded 24 ramets representing approximately 15 genets. In several cases, two ramets were collected from one genet, one of which may have been older than the other. Therefore, the age data probably suggest that the stand was younger than it actually was. The range of ages was from two to 50 years, the mean 19 years (Figure 20). Five of the ramets were over 30 years old; the younger ramets probably originated from buried portions of the shrubs. This stand appeared to be a mature stand being eroded away, as indicated by the presence of numerous old shrubs, long sections of exposed roots emerging from the ground while still attached to live branches and the lack of

Figure 16. Overview of stand L in early spring just as buds are beginning to break dormancy. Note the white branches; they have been stripped of bark.

Figure 17. Close-up of an individual shrub from stand L in early spring.

Figure 18. Willow from stand L beginning to leaf out.

Figure 19. Willow from stand L. Although the leaves have been removed from the new shoots by caribou, this shrub is a good example of the vigorous growth produced by the shrubs in this stand during 1980.

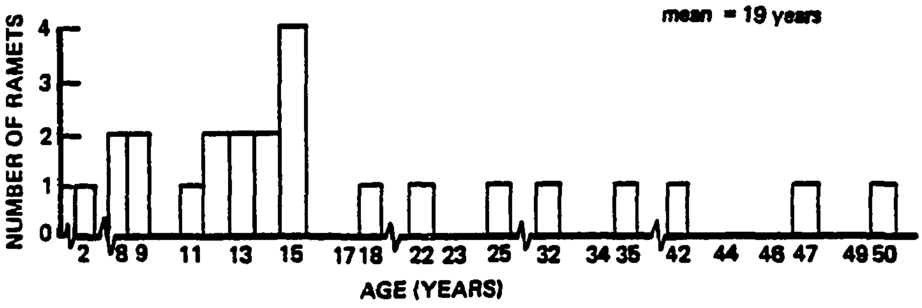

Figure 20. Age transect data from stand L, site 120-0. The sample consisted of 24 ramets collected from 15 genets.

associated taxa.

The associated taxa which were sparse and provided approximately two percent cover were *Epilobium latifolium*, grasses, *Hedysarum Mackenzii*, *Lupinus arcticus*, *Oxytropis deflexa*, *Astragalus alpinus*, and moss. *Epilobium latifolium* had a slightly higher cover value than the other taxa.

Stand Y

Stand Y was a small area of *S. alaxensis* saplings existing near the mouth of a small tundra stream. This area resembled a low gravel community, with a moist substrate composed of large gravel and few fine particles (Figure 21). However, the density of saplings was much higher than sapling density observed in low gravel communities. This high density may have been the result of a combination of factors such as a suitable substrate, adequate moisture, proximity to a seed source and distance from disturbance due to minor fluctuations in the water level of the Sag River.

Stands O and T

The river influences the pattern of community development in numerous ways. One way might be exhibited by stands O and T. Stand O, a mature stand as judged by the large shrubs it contained, was similar to transition stands in its shrub vigor and gravel substrate. Stand T was a high gravel stand. In both communities O and T, *S. alaxensis* shrubs formed a line contouring the lower edge of the community (Figure 22). This pattern may have resulted from influences of the

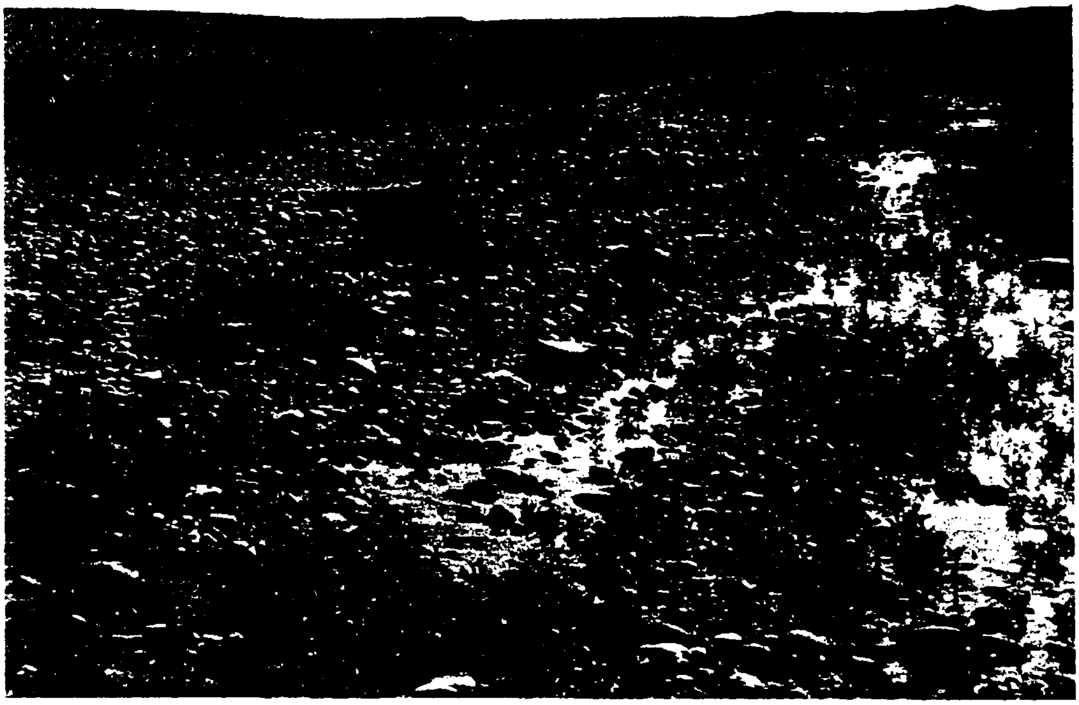

Figure 21. High density of *Salix alaxensis* saplings at the mouth of a small tundra stream (lower right corner), stand Y at 120-0.

Figure 22. Example of shrubs growing along contour of side channel, (from left to right in upper half of photo) stand T, 120-0.

river's water level during the year the shrubs were becoming established, from water movement or channelization processes that have occurred since establishment, or from some other factors that affect successful establishment and survival of *S. alaxensis*. Silt deposits and many herbs occurred along with the line of shrubs. The shrub line along the main river channel in Stand O appeared to absorb the impact of major flooding. The shrubs showed signs of abrasion, and one shrub had a large rock deposited on it (Figure 23).

Stand C

Stand C, located on an elevated, rarely flooded area, separated from other communities by high water channels, differed from the mature community type in both the shrub and herb strata. The stand was more senescent than the general mature community type. *Salix alaxensis* shrubs contained many dead ramets and provided little cover. *Salix glauca-brachycarpa* was the dominant shrub and other important shrubs were *S. hastata*, *S. lanata* and *Shepherdia canadensis*. The herbaceous layer composed of herbs, prostrate shrubs and moss was very dense compared to the mature community type. Four taxa found in this stratum that were particularly widespread were *Arctostaphylos alpina*, *Lupinus arcticus*, *Pyrola* spp. and mosses.

Branching Pattern

A small scale branching pattern study was conducted on ramets of feltleaf willow from those intensively sampled communities at 120-0.

Figure 23. Rock deposited on willow, stand O, 120-O, spring 1980.

The results are presented in Appendix A.

Examination of numerous feltleaf willow stems revealed that the shoot tips regularly abort and successive growth occurs from lateral buds. This form of growth is termed sympodial, i.e., a single axis is formed by growth from a succession of lateral meristems (Hallé, Oldeman and Tomlinson 1978).

In addition to regular shoot tip abortion, dehiscent branches, which persist for only one or two growing seasons, were found on ramets of all ages and in all branch orders. Two seventh order dehiscent branches were the highest order of branching noted on any of the ramets; these branches occurred on a 28 year old ramet.

The pattern of branching varied greatly; environmental factors such as flood damage and browsing by moose and ptarmigan influence the branching pattern of individual shrubs. Generally, however, the older the ramet the more complex the branching pattern.

Zasada (personal communication) stated that in the Interior of Alaska, ramets of *S. alaxensis* do not become as old as the ramets, for example, along the Sag River. *Salix alaxensis* is normally classified as an early successional species in the Interior but it appears to play a wider role in the arctic floodplain environment. The complex structure exhibited by the northern shrubs is more like that of a climax species. The sixth or seventh order is about the highest order of branching found in vegetation of temperate zones and this is generally confined to species considered to be climax.

Site 122-3

Introduction

The intensive study site 122-3 is approximately twelve miles north of site 120-2. It is located adjacent to a material site on a large point bar (Figures 24 and 25). The mining activities that occurred in the material site seemed to have removed portions of the mature S. *alaxensis* community. Mining activities did not appear to have disturbed the other willow communities and disturbance, if any, appears to have been minimal.

The willow communities on this point bar were flooded periodically by the Sag River, which was largely unbraided along this section having only one small island at the southern end of the site. The point bar had begun to build at the southern end of the site; it was narrow at the upstream end, became wider further downstream, and finally widened into a large gravel bar. The northern boundary of the site was located where the river cuts a side channel across the gravel bar during high water (Figure 24).

During high water, the low gravel Stand A and the lower portions of Stand D were flooded early. Since the gravel bar generally sloped up from the river, the rising floodwater progressed up the slope. One exception occurred in Stand C. Water backed up into Stand C from the northern end and subterranean water surfaced at the southern end. Water flowed through this community when portions of the high gravel

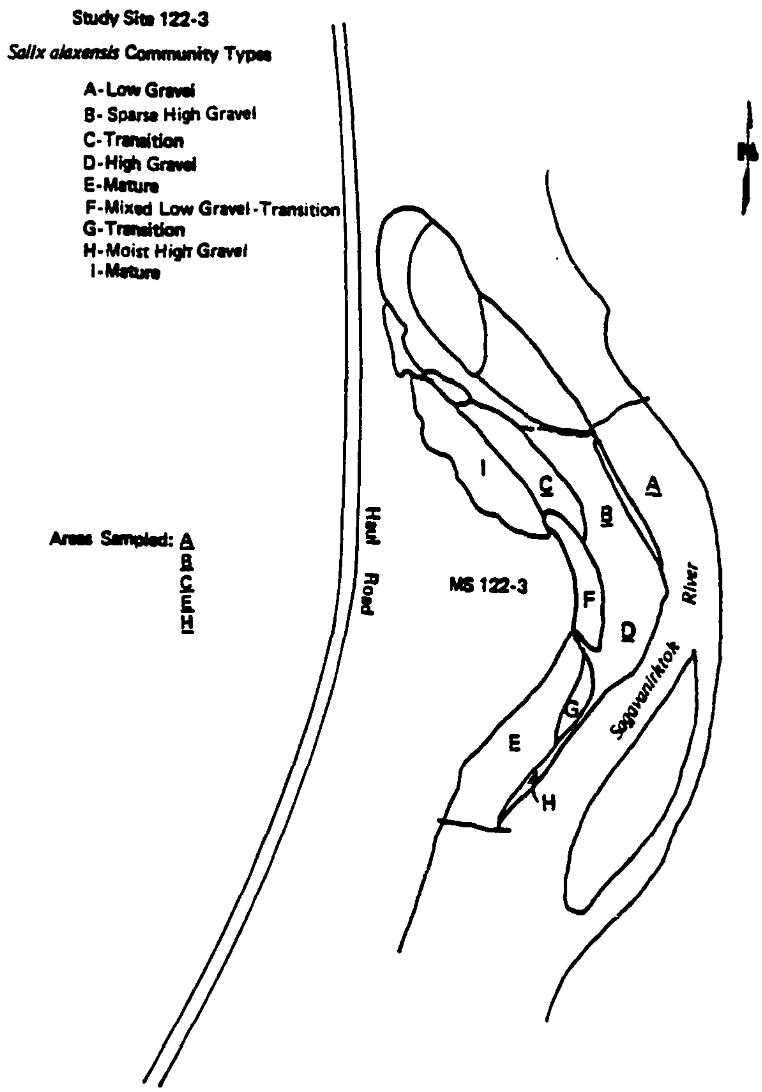

Figure 24. Map of study site 122-3

Figure 25. Aerial photograph of site 122-3 (1977).

community B were not flooded.

Observations made in March 1980 revealed that much of the area was covered with aufeis during the winter and early spring. Whether aufeis occurred at 122-3 regularly was unknown, but the presence of aufeis probably affected the flooding patterns associated with spring thaw and subsequent impacts.

Three communities sampled in 1979 and 1980 were low gravel Stand A, high gravel Stand B, and transition Stand C. Mature Stand I was sampled in 1979 only and mature Stand E and high gravel Stand H were sampled only in 1980.

Low Gravel Stand A

This community occurred along a low-lying strip of gravel next to the river in the northern third of the study site (Figure 24). The area was frequently flooded, and at times disturbance was severe, e.g. of twenty plots established in 1979 and marked in diagonal corners with 18 inch survey stakes, only nine were found in 1980 and most of them had only one stake remaining. Many saplings in the stand had been partially eroded, or partially buried by rocks or silt.

The total vegetative cover for the community was less than five percent in both 1979 and 1980. Distribution patterns were also similar for both years; *Epilobium latifolium* was the most widespread taxon followed by *S. alaxensis*. Other taxa occurred infrequently

(Tables 5a, 5b, 9a and 9b). Comparison of the two year's data reveals some interesting differences. Fewer species were recorded in the plots in 1980 than in 1979. Taxa common to both years were *Salix alaxensis* saplings, grasses, *Epilobium latifolium*, *Aster sibiricus*, *Equisetum variegatum* and moss. Those taxa occurring in the plots in 1979 but not in 1980 were *S. alaxensis* seedlings, *Hedysarum alpinum*, *Crepis nana*, *Artemisia* spp., and an unknown herb. These plants may have died, have been eroded or buried during flooding or they were not recorded in the plots because many of the plots had to be relocated. *Salix alaxensis* seedlings were not observed in the 1980 plots at all while 50 seedlings were counted in the 1979 plots. The lack of seedlings in 1980 could have been the result of high water which inundated the community during seed dispersal and the period shortly after.

The *S. alaxensis* saplings in this low gravel community were less than .25 meter tall (Table 10). Slightly fewer saplings were recorded in 1980 than in 1979 (15 and 21, respectively). The saplings were in various conditions: eroded and stretched along the gravel, buried by gravel and silt, or upright.

The substrate was characterized by large gravel, most approximately 30 centimeters in diameter and few fine particles (Tables 11 and 12). Comparison of the data for the two years suggests that gravel sizes might have been slightly larger in 1980, probably resulting from the relocation of plots or from new gravel deposits. A new deposit of small gravel did occur during spring flooding just

Table 9a. Percent cover of species occurring on selected floodplain sites on the Sag River, tributaries of the Sag River and adjacent drainages (1979)

	Percent cover of species found in square meter plots (based on 20 1-meter square plots unless otherwise noted)																				
	113-2			MS 120-2B			112-3			Happy Valley			Oks Creek		Kuparuk River		Flood Creek		Atigun River	
	L.G.[1]	H.G.[1]	T[1]	L.G.	H.G.	T	L.G.	H.G.	T	L.G.	H.G.	T	L.G.	H.G.	L.G.[3]	H.G.[4]	L.G.	H.G.[4]	L.G.	H.G.[4]
Salix alaxensis	1	4	20	+	7	11	+	1	7	+	8	8	+	3	4	5	5	10	1	2
S. glauca-brachycarpa	+[2]	+	1			+		+	+			+								+
S. hastata	+	+	+			+		+	+			+			+		+	+		+
Shepherdia canadensis																				
Salix lanata						+											+			
S. arbusculoides						+								1						
Rosa acicularis														1						
No. of seedlings																				
Salix alaxensis	125	5		10		15	50	5	850	50				5			30		100	
Salix spp.							5					350			75			10		
Arctostaphylyos alpina			+														+			
Salix arctica																				+
Salix reticulata																	+			
Rhododendron lapponicum		+																		
Gramineae	+	1	+	+	+	1	+	+	1	+	+	2	+	5	1	1	+	+	+	1
Epilobium latifolium	+	9	+	+	1	+	1	+	+	+	5	2	1	8	8	1	1	6	3	1
Hedysarum Mackenzii		+	+		7	8		1	+		5	1		+					1	2
H. alpinum	+	+	2		+	2	+	+	+		+	+	+	+				+		+
Aster sibiricus			+			1	+	+	+	+	+	1		+						
Castilleja caudata					+	+		+	+		+	+		+						
Senecio spp.		+	1		+	+						+		+	+					
Astragalus or *Oxytropis* spp.	+	1	8	+	+	2			+		+	1			+				+	+
Lupinus arcticus						+					+									
Astragalus spp.					1			+	+		+			+						+
Polygonum viviparum		+							+						+				+	+
Juncus spp.									+			+							+	
Artemisia spp.	+				+		+	+			+		1	5	+	+			+	
Pedicularis spp.		+										+								
Melandrium sp.		+																	+	
Papaver sp.		+														+				
Saxifraga sp.															+	+				
Erigeron sp.															+					
Potentilla sp.																	+	+		

Table 9a. Continued.

	Percent cover of species found in square meter plots (based on 20 1-meter square plots unless otherwise noted)																			
	113-2			MS 120-2B			112-3			Happy Valley			Oks Creek		Kuparuk River		Flood Creek		Atigun River	
	L.G.[1]	H.G.[1]	T[1]	L.G.	H.G.	T	L.G.	H.G.	T	L.G.	H.G.	T	L.G.	H.G.	L.G.[3]	H.G.[4]	L.G.	H.G.[4]	L.G.	H.G.[4]
Equisetum variegatum				+	+	+	+	+	1	+		1		+			+	+		
Caryophyllaceae	+	+				+		+		+		+	+	+	1	+	+		+	
Equisetum sp.	+								+			+							+	
Carex spp.									+			+			+					
Crepis nana	+	+		+	+		+	+		+	+	+	+		+	+	+	+	+	+
Parnassia spp.										+		+								+
Anemone parviflora																		+		
Gentiana spp.									+											
Dryas integrifolia		+	+						+											
Galium sp.			+																	
Unknown herb	+	+		+			+	+	+	+				+	+		+	+	+	+
Dryas Drummondii																	+	+		
Moss	+	2	25	+	2	5	+		+	+	1	1		2	2	+	2	+	+	1
Lichen		+	2			+										+				
Liverwort												+					+			
Unknown																				
Algae	+														+					
Fungi																		+		
Total vascular plant species and groups	2	18	12	7	12	16	9	16	19	9	12	19	7	15	14	8	13	11	13	15
Total species and groups	14	20	14	8	13	18	10	16	20	10	13	21	7	16	16	10	15	13	14	16
Total cover (percent) (3 +'s = 1%)	5	22	62	3	21	35	4	7	15	3	21	21	4	28	20	9	12	20	12	11

[1] L.G., H.G. and T. represent low gravel, high gravel and transition community types respectively.

[2] + Represents a value less than one

[3] Based on 11 plots.

[4] Based on 10 plots.

Table 9b. Percent frequency of vascular and non-vascular plant species occurring on selected floodplain sites on the Sag River, and adjacent drainages

	Percent frequency of species found in square meter plots (based on 20 1-meter square plots unless otherwise noted)																			
	113-2			MS 120-2B			112-3[2]			Happy Valley			Oks Creek		Kuparuk River		Flood Creek		Atigun River	
	L.G.[1]	H.G.[1]	T[1]	L.G.	H.G.	T	L.G.[3]	H.G.	T	L.G.	H.G.	T	L.G.	H.G.	L.G.[4]	H.G.[5]	L.G.	H.G.[5]	L.G.	H.G.[5]
Salix alaxensis	75	70	75	20	80	75	58	35	55	95	85	95	15	35	45	50	180	100	75	60
S. glauca-brachycarpa	10	10	5			5		5	10			20								10
S. hastata	15	5	5			5		5	15			40			27		45	10		10
Shepherdia canadensis																				
Salix lanata						5											5			
S. arbusculoides						5								5						10
Rosa acicularis														5						
Seedlings																				
Salix alaxensis	40	5		20		10	65	5	65	70				5			10		15	
Salix							5					75			18			10		
Arctostaphylyos alpina			10														5			
Salix arctica																				30
Salix reticulata																	5			
Rhododendron lapponicum		5																		
Gramineae	65	40	10	30	50	60	26	40	70	55	35	95	25	85	73	60	30	40	55	60
Epilobium latifolium	55	100	35	25	30	5	74	70	45	50	55	70	45	95	91	70	55	80	50	10
Hedysarum Mackenzii		10	25		95	85		55	25		55	50		5					15	40
H. alpinum	5	30	50		5	35	10	15	30		30	5	5	15				10		10
Aster sibiricus			15			40	5	20	25	5	20	40		10						
Castilleja caudata					5	5		5	15		10	35		5						
Senecio spp.		5	15		5	15						5		30	9					
Astragalus or *Oxytropis* spp.	30	55	100	5	35	85			10		15	40			27				15	50
Oxytropis spp.								10												10
Lupinus arcticus						10					5									
Astragalus spp.					55			5	15		5			35						20
Polygonum viviparum		5							5						18				5	10
Juncus spp.									20			35							5	
Artemisia spp.	5				10		11	5			30		40	85	55	20			20	
Pedicularis spp.		5										5								
Melandrium sp.		5																	5	
Papaver sp.		5														10				
Saxifraga sp.															27	10				
Erigeron sp.															18					
Potentilla sp.																	5	10		

Table 9b. Continued.

	113-2			MS 120-2B			112-3[2]			Happy Valley			Oks Creek		Kuparuk River		Flood Creek		Atigun River	
	L.G.[1]	H.G.[1]	T[1]	L.G.	H.G.	T	L.G.[3]	H.G.	T	L.G.	H.G.	T	L.G.	H.G.	L.G.[4]	H.G.[5]	L.G.	H.G.[5]	L.G.	H.G.[5]
Equisetum variegatum				65	5	10	32	15	75	20		90		5			35	50		
Caryophyllaceae	20	5				10			15	5		35	15	10	91	30	10		10	
Equisetum sp.	10								20			20							5	
Carex spp.									10			10			27					
Crepis nana	45	5		15	25		5	15		5	10	5	15		9	10	10	5	5	10
Parnassia spp.										5		20								10
Anemone parviflora																		10		
Gentiana spp.									5											
Dryas integrifolia		10	10						5											
Galium sp.			5																	
Unknown herb	35	20		15			11	20	10	15				25	36		25	30	10	10
Dryas Drummondii																	10	10		
Moss	60	80	95	45	70	85	42		15	85	90	55		75	36	30	95	100	20	50
Lichen		15	85			5										10				
Liverwort												30					5			
Algae	15														9					
Fungi																		10		

Percent frequency of species found in square meter plots (based on 20 1-meter square plots unless otherwise noted)

[1] L.G., H.G. and T. represent low gravel, high gravel and transition community types respectively.

[2] The L.G., H.G. and T. stands at 122-3 are also referred to as stands A, B and C respectively. The L.G. and H.G. stands at Happy Valley referred to as stands A and B respectively.

[3] Based on 19 plots.

[4] Based on 11 plots.

[5] Based on 10 plots.

Table 10. Summary of *Salix* shrub heights by community type for 122-3, 1980
Values are percent of willows in each size class.

Stand	Number of Shrubs	Shrub Height (meters)					
		<.25	<.50	<.75	<1.0	<1.5	>1.5
S. alaxensis							
Low Gravel A	14	100	0	0	0	0	0
High Gravel B	14	71	29	0	0	0	0
High Gravel H	93	72	26	2	0	0	0
Transition C	17	29	47	6	0	18	0
Mature E	34	0	15	15	44	24	2
S. hastata[1]							
High Gravel B	7	100	0	0	0	0	0
High Gravel H	12	100	0	0	0	0	0
Transition C	17	100	0	0	0	0	0
Mature E	14	14	36	29	21	0	0
S. glauca-brachycarpa							
High Gravel B	3	100	0	0	0	0	0
High Gravel H	1	100	0	0	0	0	0
Transition C	7	86	14	0	0	0	0
Mature E	33	29	29	14	14	14	0

[1] Only stands containing *Salix* spp. other than *S. alaxensis* are listed here.

Table 11. Summary of largest gravel size found in plots at 122-3, 1980
Values are percentage of plots in each size category.

	Gravel Size				
Community Type	0-10cm	≤20	≤30	≤40	≥40
Low Gravel A	0	5	65	20	10
High Gravel B	15	35	50	5	0
High Gravel H	0	10	25	40	25
Silt Transition C	75	10	15	0	0
Mature E	100	0	0	0	0

Table 12. Percentage of gravel in plots
Values are percent of plots in each size category.

	Percent Gravel					
Community Type	0%	≤25	≤50	≤75	≤90	≤100
Low Gravel A	0	0	0	0	5	95
High Gravel B	15	0	10	20	25	35
High Gravel H	0	5	5	35	45	10
Silt Transition C	70	25	5	0	0	0
Mature E	100	0	0	0	0	0

south of the low gravel community. The gravel was initially deposited on top of some aufeis and remained when the ice melted.

High Gravel Stands

Stand B

The high gravel Stand B at 122-3 was located approximately one-half meter higher than the low gravel Stand A on a relatively flat portion of the gravel bar (Figure 24). Because of its elevation, it was disturbed less frequently than the low gravel community, but disturbance did occur. Half of the plots established in 1979 were missing in 1980 and had to be relocated. Vegetation was sparse, and consistent with the general description of high gravel communities; the most important species, *S. alaxensis*, *Hedysarum Mackenzii* and *Epilobium latifolium*, grew on a rocky substrate which contained a few large silt patches.

The total plant cover was approximately seven percent in Stand B, which was slightly higher than the total cover found in low gravel Stand A; however, the diversity of taxa was greater in Stand B (Table 5a). All taxa observed in the low gravel stand were also found in the high gravel stand; the new taxa in Stand B were *S. glauca-brachycarpa*, *S. hastata*, *Hedysarum Mackenzii*, *H. alpinum*, *Castilleja caudata*, *Polygonum viviparum*, *Astragalus aboriginum*, and *Crepis nana*.

Comparison of the data from 1979 and 1980 reveal only minor differences even though half the plots were relocated (Tables 5a, 5b, 9a and 9b). A slightly higher cover was observed in 1980 than in 1979 for *Epilobium latifolium; Artemisia* spp. was not found in the plots in 1980; moss was in the 1980 plots but not in the 1979 plots; and one *S. alaxensis* seedling was observed in 1979 compared to the 75 seedlings observed in 1980. Although slight variations in frequency occurred between 1979 and 1980, those taxa with the highest frequencies in 1979 also had the highest frequencies in 1980; these taxa were *Epilobium latifolium, Hedysarum Mackenzii,* grasses, *Salix alaxensis* and *Equisetum variegatum.*

General characteristics of the *S. alaxensis* shrubs in this high gravel stand include a mean age of six years (Figure 26), 70 percent of the shrubs are less than .25 meter and 30 percent are between .25 and .50 meters in height (Table 10). Shrub size appears to be slightly larger in the northern end of the stand, and on the edge of the stand away from the river. A similar pattern was observed in the mature community at 120-0.

The high gravel Stand B had more silt and sand on the surface than did the low gravel Stand A. Gravel sizes were also slightly smaller with 90 percent of the gravel less than 30 centimeters in diameter (Tables 11 and 12). The substrate surface appeared to be dry during much of the summer; the silt and sand areas at times became quite powdery. Such dryness could be detrimental to seedling germination and establishment.

Figure 26. Age transect data from high gravel stand B, site 122-3. The sample consisted of 23 ramets collected from 23 genets.

Stand H

The high gravel community H occurred along a narrow strip of gravel at the southern end of the study area. The gravel strip began where the river started to curve to the east, causing the cutting action of the west bank to stop and the building of a gravel bar to begin. The strip was narrow at first and became wider further north as it approached Stand D (Figure 24). The gravel sloped upward from the river to the level of the mature stand. The community was subject to frequent inundation, particularly along the lower edge. Vegetation was evenly distributed and moderately dense for high gravel communities observed in this study. The substrate appeared moist most of the season.

The diversity of taxa did not differ much between high gravel Stand H and B (Table 5a); four additional taxa were recorded in Stand H: *Senecio* spp., *Oxytropis campestris*, *O. borealis* and *Stellaria* sp. The major difference between the two stands was in percent cover; Stand H had double the cover values of Stand B, chiefly due to *Salix alaxensis* and *Epilobium latifolium*. In Stand H, the cover values for these two species were seven and four percent, respectively, and in Stand B the cover value was one percent for each species. The taxa, particularly *S. alaxensis*, *Shepherdia canadensis*, grasses, *Equisetum variegatum* and moss, tended to be more widely distributed in Stand H than in Stand B; except for *Hedysarum Mackenzii* which had a much narrower distribution.

The *S. alaxensis* shrubs in high gravel Stand H tended to be slightly taller than the shrubs in Stand B; two percent of Stand H's willows were .50 to .75 meters tall, whereas none of Stand B's willows were that tall (Table 10). The mean age of shrubs in Stand H was seven, one year older than in Stand B (Figure 27).

Gravel size tended to be larger in Stand H than in Stand B, with 25 percent of the gravel greater than 40 centimeters in diameter, and fewer and smaller areas of silt-sand deposits occurring in Stand H. The substrate appeared to be moist which might contribute to the higher density of vegetation observed in this stand. Close proximity of the river on one side of the stand and the mature willow community, where soils were colder and retained moisture longer, on the other side, probably contributed to the higher moisture levels.

Transition Stand C

The transition community C was immediately west of the high gravel Stand B. To the west of C was the mature community I (Figure 24). Stand C was lower than the two communities on either side and was subject to more frequent disturbance by flooding than either of the adjacent communities. Only half of the plots established in 1979 were relocated in 1980.

The stand was characterized by *S. alaxensis* shrubs that had been eroded on the upstream side and had silt deposits occurring on the downstream side. This gave the shrubs the appearance of growing on a mound of soil. The few *S. alaxensis* shrubs in the community

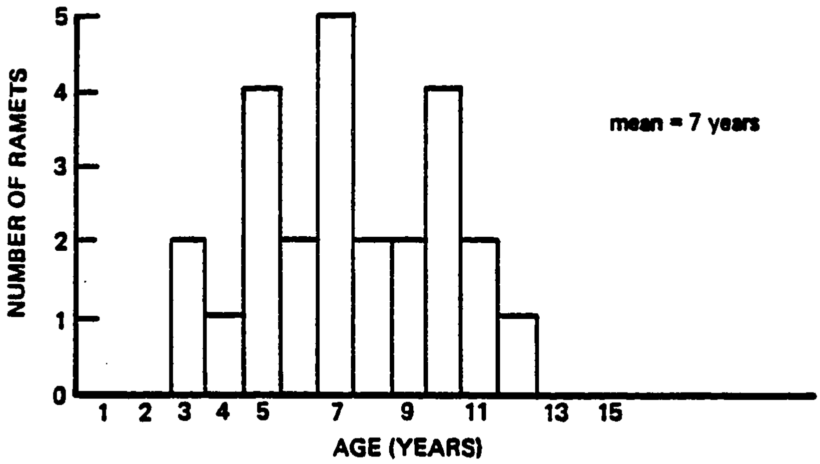

Figure 27. Age transect data from high gravel stand H, site 122-3. The sample consisted of 25 ramets collected from 25 genets.

appeared to be distinct from each other and well separated by a generally barren silty-sand surface.

The number of taxa present in the plots in 1979 and 1980 differed by one, but greater differences existed in the composition of the taxa present each year (Tables 5a, 5b, 9a and 9b). Three taxa that were observed in 1979 but not in 1980 were *Dryas integrifolia*, liverwort, and an unknown herb. Five taxa present in 1980 and not in 1979 were *Vaccinium uliginosum, Salix arctica, Crepis nana, Parnassia* spp., and *Gentiana* spp. The relocation of plots or the erosion or burial of plants could explain these differences. Many of the taxa associated with *S. alaxensis* were found at the base of the shrubs or in an area somewhat protected from flooding. Cover may have increased slightly from 1979 to 1980.

Variation in distribution patterns between 1979 and 1980 was small. Comparison of transition Stand C to high gravel Stands B and H showed that similar taxa, *S. alaxensis*, grasses, *Equisetum variegatum* and mosses, continued to be the most widespread. Although still widespread, *Epilobium latifolium* had narrowed its distribution and *Equisetum* spp., *Juncus* spp. and *Aster sibiricus* had broadened their distribution.

Salix alaxensis seedlings were observed both in 1979 and 1980 (825 and 625 total seedlings, respectively). The moist silt and sand provided a good germinating medium but once it dried, which occurred quickly, the surface became hard with a baked surface causing high mortality among the seedlings (Figure 28). Several

Figure 28. High density of seedlings on a baked silt substrate in stand C, 122-3.

observations were made of such occurrences which might help to explain the lack of *S. alaxensis* saplings in the stand. Comparison of transition Stand C data with the high gravel Stands B and H showed slightly greater diversity and a shift in species composition for the transition stand (Table 5a). Stand C contained the taxa *Juncus* sp., *Carex* sp., *Gentiana* spp., *Parnassia* spp. and *Equisetum* species other than *E. variegatum*. These taxa, which were not found in the two high gravel stands, tended to be more common in areas of silty-sandy soils that were not well drained. The growth form of the shrubs found in transition Stand C and high gravel Stand H differed considerably, but the cover values did not vary greatly (11 and 7 percent, respectively).

The shrubs in Stand C were generally vigorous and of medium height with many emergent ramets extending over large areas. The shrubs expanded by layering; branches, particularly those occurring on the downstream side of the shrub, were buried by silt and subsequently produced new shoots and roots. In this way individual genets covered large areas. Some of the ramets from these large individuals were very young and when ramets collected for age analysis included these young ramets, the age of the population seemed to be much younger than it actually was.

The mean age of the ramets collected from Stand C was ten years. Ages ranged from 3-18 years (Figure 29). These ages were only slightly higher than the ages for the high gravel Stands B and H. Seventy-five percent of the shrubs were less than .50 meter tall and a few shrubs approached 1.5 meters in height (Table 10).

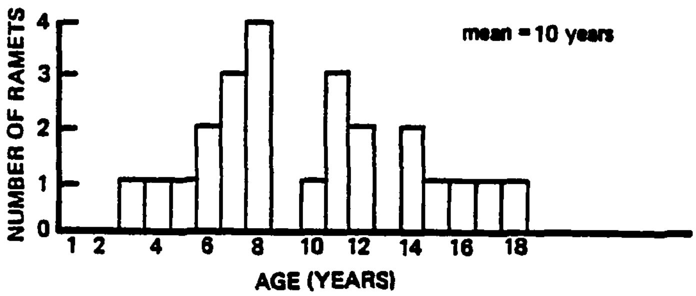

Figure 29. Age transect data from transition stand C, site 122-3. The sample consisted of 24 ramets collected from 12 genets.

The substrate was primarily silt and sand with a few areas containing gravel less than 30 centimeters in diameter (Tables 11 and 12).

Mature Stand E

The mature Stand E was located at the southern end of the study area adjacent to the high gravel community H (Figure 24). The western boundary of the stand was the edge of the material site. Stand E generally appeared to be disturbed infrequently by flooding except for a narrow strip along the eastern edge of the stand, which had more sand and mineral surface exposed. Also shrubs appeared to be somewhat eroded on the upstream side with silt and sand deposited on the downstream side. The rest of the stand had a more uniform surface of silt and sand that supported fairly dense vegetation.

The mature Stand E had the highest diversity and highest cover of any of the communities sampled at 122-3 and several taxa were more widespread, ten taxa were found in at least half of the plots compared to two, two, five and three taxa for Stands A, B, H and C, respectively (Table 5a and 5b). Twenty-eight taxa were represented for a total cover of approximately 90 percent. In the mature stand, *Salix glauca-brachycarpa*, *S. hastata*, grasses, *Hedysarum Mackenzii*, *H. alpinum*, *Aster sibiricus*, *Senecio* spp. and mosses had greater cover than in other stands at 122-3. The large cover value of 19 percent for mosses suggested that the mature community was more moist than any of the other community types. *Shepherdia canadensis*, *Arctostaphylos alpina*, *Petasites* sp., *Anemone parviflora*, *Pyrola asarifolia*, *Dryas integrifolia*, lichens, liverwort and algae occurred only in the mature stand. One taxon, *Epilobium latifolium*, had lower cover and frequency particularly when compared to the high gravel Stands B and H.

The *S. alaxensis* in Stand E contained moderate to large amounts of dead wood; the percent of dead wood increased and the abundance and vigor of *S. alaxensis* decreased toward the southern and eastern edges of the stand. Shrubs ranged in size from .25 to greater than 1.5 meters tall and nearly fifty percent of the shrubs were .75 to 1.0 meter tall (Table 10). Some *S. hastata* and *S. glauca-brachycarpa* shrubs approached the heights of *S. alaxensis* shrubs reaching nearly 1.0 and 1.5 meters tall respectively. The ages of the shrubs in Stand E were represented by 25 ramets from approximately 16 genets; the mean age was 23 years. The range of ages was from 13 to 37 years (Figure 30).

Other Stands

Four *S. alaxensis* communities existed at site 122-3 other than those just described (Figure 24). All were qualitatively described and particularly important aspects of each will be discussed below.

Stand D

Stand D was a high gravel community somewhat intermediate in traits between Stands B and H. The substrate consisted primarily of

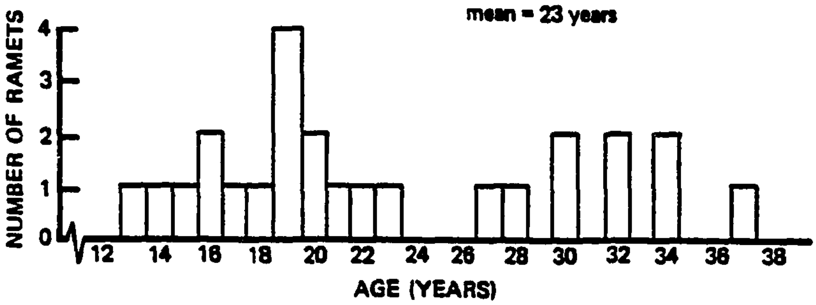

Figure 30. Age transect data from mature stand E, site 122-3. The sample consisted of 25 ramets collected from 16 genets.

large rocks sloping from Stand F to the river. Legumes, particularly *Hedysarum Mackenzii* and *Astragalus aboriginum*, and *S. alaxensis* were the dominant species. These plants were more uniform in size and distribution than those found in Stands B and H. The size of *Salix alaxensis* shrubs in Stand D more closely resembled that found in Stand B but density was higher. Three large feltleaf willow occurred in the area of Stand D near the low water level of the river. These shrubs differed in size from the rest of the shrubs in the stand which suggested that the shrubs may have originated from vegetative material deposited on the gravel bar. One shrub was excavated; the appearance of the root and lower stem mass suggested that it had originated on that site as a seedling or if vegetative material had given rise to the shrub, there was no apparent evidence left. The question of why were three shrubs so different from other shrubs in the stand remained unanswered.

Stand F

Stand F contained *S. alaxensis* shrubs similar to those of several other community types (Figure 31). The stand was open and the surface was primarily large gravel substrate with few fines; it was removed from the river and probably was inundated only during floods associated with spring thaw. Large shrubs, some taller than two meters with shorter ramets on the downstream side, were mixed with small saplings typical of a low gravel community. Some shrubs were vigorous, others were not. The vigorous shrubs showed long new

Figure 31. Stand F, site 122-3: Note wide range of shrub sizes.

shoots and dense foliage and less vigorous shrubs showed shorter new growth, small amounts of dead wood and sparse foliage.

The diverse characteristics of this community prompted the excavation of two shrubs to determine whether the shrubs originated from seed or from buried vegetative material. The shrubs were growing very close to each other, were not particularly vigorous and had a small amount of dead wood at their base. The excavation revealed that the shrubs were separate individuals originating from buried branches (Figure 32). The branches were excavated to an approximate depth of one meter and length of one and a half meters. Buried branches extended beyond that depth but excavation stopped because the branches were decayed.

It appeared that shrubs of widely differing ages could be growing in this stand and that age might be a very important factor in explaining the differences in vigor between shrubs. The discovery of these deeply buried branches which gave rise to new shrubs reiterates the importance of river dynamics to riparian vegetation.

Stand G

Stand G was a transition stand with a primarily gravel substrate. Some silt and sand colonized by moss occurred between the rocks. The major herbaceous taxa were legumes, particularly *Astragalus* spp. and *Oxytropis* spp. *Salix alaxensis* size and vigor were similar to those in other transition communities. As distance from the river increased within the stand, density of *S. alaxensis*,

Figure 32. Willows excavated in stand F, site 122-3.

S. glauca-brachycarpa and *Shepherdia canadensis* increased, *Salix alaxensis* height decreased and more silt was present.

Stand I

Stand I did not differ greatly from other mature stands. *Salix alaxensis* was generally more senescent than in mature Stand D and other willows increased in amount with distance from the river. Of the three study sites, 122-3 contained the only spatially continuous gradient of young to old *S. alaxensis* communities. The communities progressed from low gravel Stand A at the river's edge to high gravel Stand B, transition Stand C and mature Stand I with distance away from the river.

Happy Valley Site

Introduction

The Happy Valley study site is located approximately 25 miles north of the 120-0 site. It was bounded on the west by a small intermittent side channel of the Sag River, on the south and east by a large channel, and on the north by the main channel (Figures 33 and 34). The small side channel disappeared only at low water levels toward the end of the summer. Flooding from this channel affected primarily the periphery of the mature stand and the small regeneration area that occurred along the side channel. Water from the larger channel along the southern and eastern boundaries first flooded the low gravel community A and then flooded Stand O (Figure 33). The flooding of Stand O probably occurred in spring. Water appeared to flow over Stand O into a pond adjacent to the silt regeneration area and then out the northern end of the gravel bar. Numerous sod clumps deposited during high water occurred in Stand O. The channel appeared to be building the gravel bar of Stand A and the southern end of Stand O, but further north along the eastern boundary the river was eroding the gravel bar. High water eroded this area more quickly than low water. At the northeast corner where the two major channels of the Sag River join, the gravel bar appeared to be building.

The western half of the study site was covered by a mature willow community with primarily a silty substrate. The eastern half and

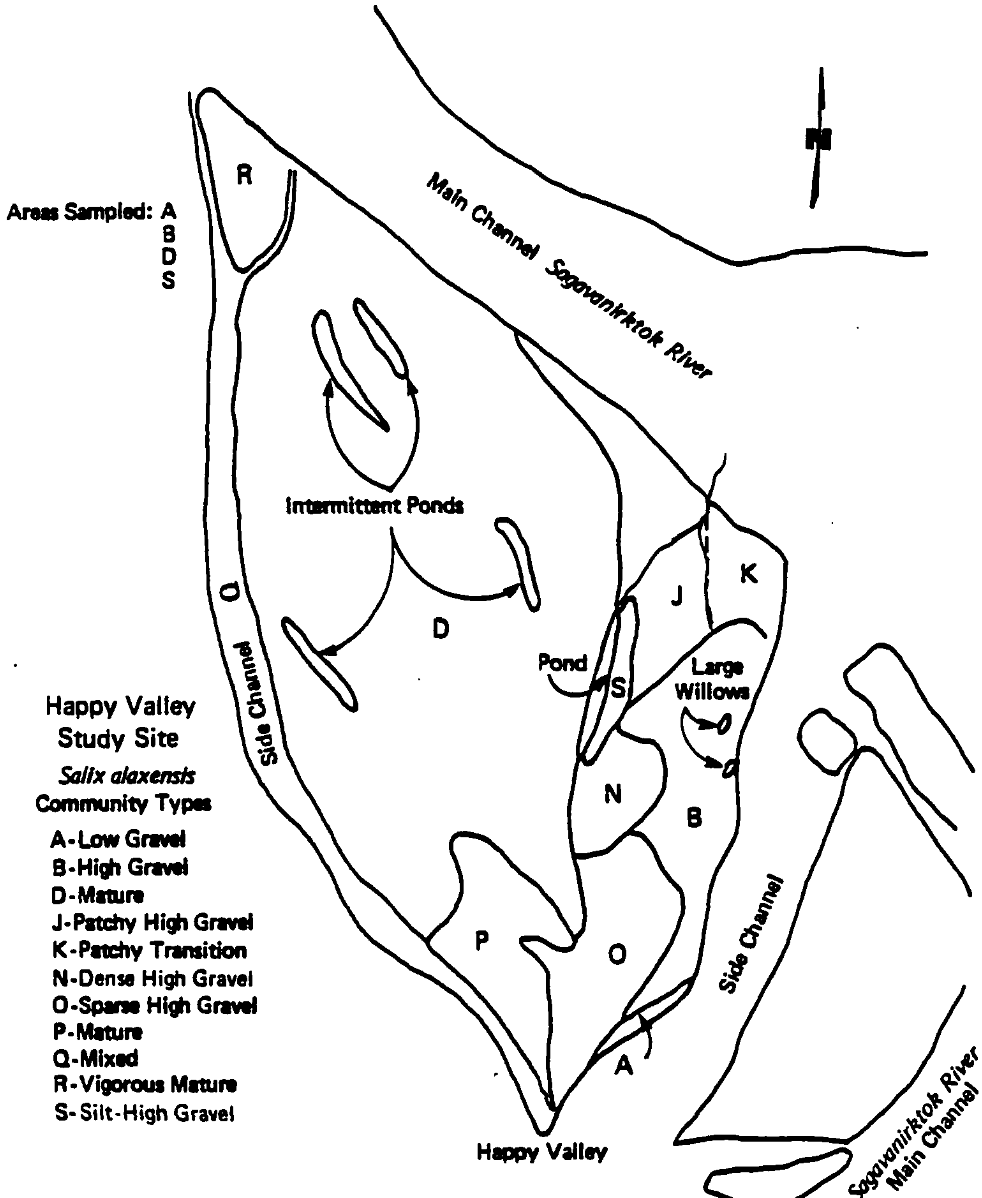

Figure 33. Map of Happy Valley study site

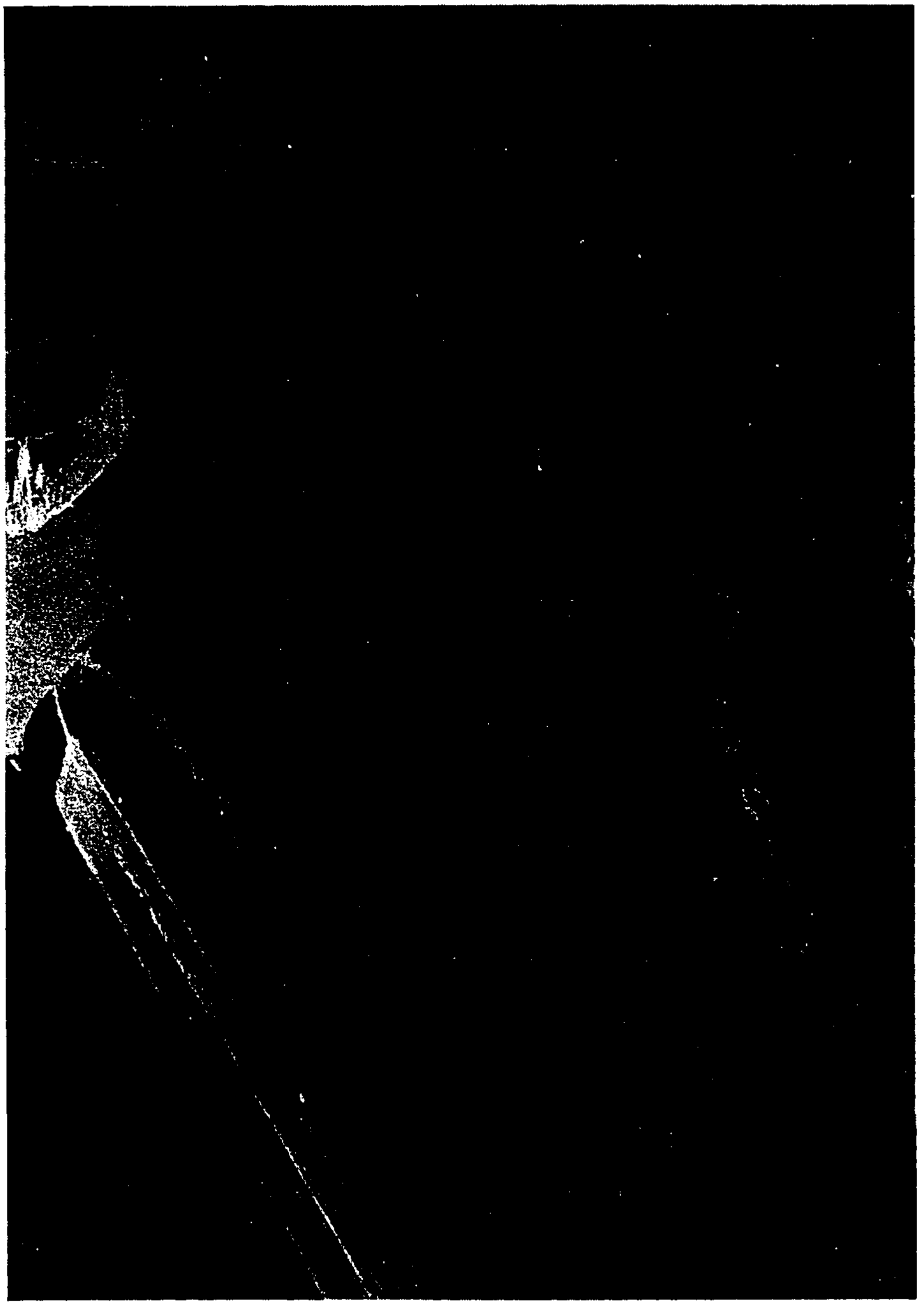

Figure 34. Aerial photograph of Happy Valley site (1980).

southern tip were occupied by young *S. alaxensis* communities. The northern quarter of the young willow communities had a silt substrate; a gravel substrate covered the remainder of the site. Happy Valley contained the patchiest vegetation of the three intensive sites, this patchiness was most pronounced in the mature stand and the silty area in the young willow communities.

Low Gravel Stand A

The low gravel Stand A occurred along the southwestern portion of the study area. It was a narrow community stretching along the river's edge much as the low gravel stand at 122-3. The stand was frequently inundated but disturbance did not appear to be severe; 90 percent of the plots established and staked in 1979 were in place in 1980. Also most of the young saplings in the stand were upright and did not give the appearance of being bent over and eroded or buried.

The Happy Valley low gravel stand was quite similar to the low gravel stand at 122-3 (Table 5a). Total vegetative cover for Happy Valley's low gravel Stand A was four percent compared to three percent for the low gravel stand at 122-3. Floristic composition also was generally similar between the two stands; common taxa were *Salix alaxensis*, grasses, *Epilobium latifolium*, *Aster sibiricus*, *Equisetum variegatum* and moss. Two taxa which occurred at the Happy Valley stand and not at 122-3 were *Crepis nana*, *Stellaria* sp.; *Astragalus alpinus* occurred at 122-3 and not at Happy Valley. Some small differences existed between the two stands in the distribution of taxa; grasses, *Equisetum variegatum* and moss were more widespread at Happy Valley and *Epilobium latifolium* was more widespread at 122-3 (Table 9b).

Comparison of the 1980 and 1979 data revealed some differences (Tables 5a, 5b, 9a and 9b). *Castilleja caudata* and *Parnassia* spp. were recorded in 1979 but not in 1980. Twice as many *S. alaxensis* saplings were recorded in the plots in 1979 as in 1980, 117 and 50 saplings, respectively. However, three times as many seedlings were recorded in the plots in 1980 as in 1979, 150 and 50 seedlings, respectively. Data were collected two weeks earlier in 1980 than in 1979 which might account for some of the difference in seedling number. Despite the apparent reduction in abundance of *S. alaxensis* saplings from 1979 to 1980 at Happy Valley, the saplings did not appear to be as severely impacted by high water as the saplings at 122-3. Density of saplings was higher at Happy Valley and seedlings were recorded at Happy Valley but not at 122-3. Plot data were collected seven days earlier at 122-3 than at Happy Valley, but were collected late enough in the season that seedlings should have been present at 122-3 if conditions had been suitable for their germination and survival.

The mean of the ramets collected for age determination in Stand A was two years with a range from one to seven years (Figure 35). Heights of *S. alaxensis* occurring within the plots of the low gravel stand at Happy Valley were largely less than 25 centimeters; two shrubs were 25 to 50 centimeters tall (Table 13).

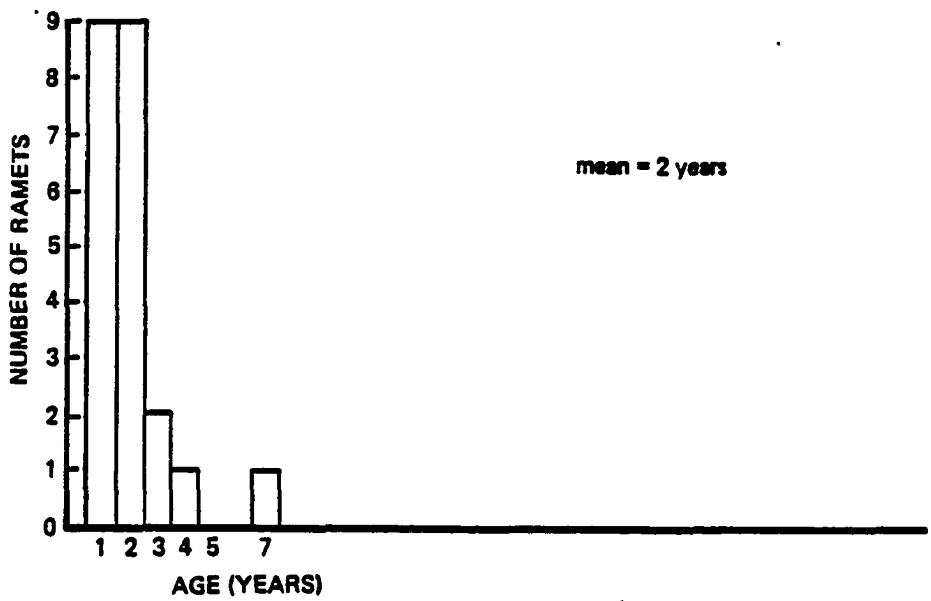

Figure 35. Age transect data from low gravel stand A, Happy Valley site. The sample consisted of 22 ramets collected from 22 genets.

Table 13. Summary of heights of willows found in plots at Happy Valley, 1980
Values are percent of shrubs in each size category.

Community Type	Total No. of Shrubs	Shrub Height (meters) ≤.25	≤.50	≤.75	<1.0	<1.5	>1.5
S. alaxensis							
Low Gravel A	57	94	6	0	0	0	0
High Gravel B	60	45	52	3	0	0	0
Mature D	23	4	13	13	26	26	18
Stand S	269	88	12	0	0	0	0
S. hastata[1]							
High Gravel B	1	100	0	0	0	0	0
Mature D	69	58	19	13	1	0	0
Stand S	376	100	0	0	0	0	0
S. glauca-brachycarpa							
High Gravel B	1	100	0	0	0	0	0
Mature D	46	30	43	20	7	0	0
Stand S	72	22	78	0	0	0	0
S. lanata							
High Gravel B	1	100	0	0	0	0	0
Mature D	1	100	0	0	0	0	0
Stand S	3	100	0	0	0	0	0

[1] Only stands containing *Salix* spp. other than *S. alaxensis* are listed here.

The substrate of the low gravel stand was generally large gravel, 10-40 centimeters in diameter with a few larger rocks. Seventy-five to 100 percent of the surface was gravel with these dimensions (Tables 14 and 15).

High Gravel Stand B

The high gravel Stand B at Happy Valley was located along the eastern side of the gravel bar and it appeared to be minimally disturbed by flooding. All of the plots staked in 1979 were found in 1980 and had no apparent flood damage. Erosion of the cutbank along the northeastern edge of the stand was the most visible effect of high water; along this area were a few *S. alaxensis* shrubs that were much larger than the shrubs in the rest of the stand.

The total vegetative cover in Stand B (36 percent) was much greater than that found in low gravel Stand A (4 percent) and was greater than the cover values found at any other high gravel stand sampled in 1980 (Table 5a). The largest contributors to cover and the most widely distributed taxa were *S. alaxensis* and *Hedysarum Mackenzii*, each with 11 percent cover, and *Epilobium latifolium* with six percent cover; mosses were also widely distributed. The remaining 16 taxa recorded in the plots provided the additional seven percent cover. Stand B contained more than twice the number of taxa found in Stand A, 19 and 8, respectively. New taxa recorded in Stand B include *Salix glauca-brachycarpa*, *S. hastata*, *S. lanata*, several legumes,

Table 14. Summary of largest gravel size found in plots at Happy Valley, 1980
Values are percent of plots in each category.

	Gravel Size (centimeters)				
Community Type	0-10	⩽20	⩽30	⩽40	>40
Low Gravel A	0	15	55	20	10
High Gravel B	0	20	70	10	0
Mature D	100	0	0	0	0
Stand S	100	0	0	0	0

Table 15. Percent gravel in plots at Happy Valley, 1980
Values are percent of plots in each size category.

	Percent Gravel					
Community Type	0%	⩽25	⩽50	⩽75	⩽90	⩽100
Low Gravel A	0	0	10	15	40	35
High Gravel B	0	0	5	30	40	25
Mature D	100	0	0	0	0	0
Stand S	100	0	0	0	0	0

Castilleja caudata, Senecio spp., and *Artemisia* spp., *Stellaria* sp. and *S. alaxensis* seedlings.

Five more taxa were found in the plots in 1980 than in 1979 and cover values were higher for some taxa in 1980 (Tables 5a, 5b, 9a and 9b). *Salix glauca-brachycarpa, S. hastata* and *S. lanata* were recorded in 1980 but not in 1979 probably because these willows had not been distinguished from *S. alaxensis* in 1979. Other taxa found in 1980 and not in 1979 were *Senecio* spp. and *Equisetum variegatum*. Slightly higher cover values were recorded for five species in 1980 compared with 1979; those species (and their 1979-1980 cover values) were: *S. alaxensis*, 8 and 11 percent; *Epilobium latifolium*, 4 and 6 percent; *Hedysarum Mackenzii*, 5 and 11 percent; moss, 1 to 2 percent; and *Lupinus arcticus*, less than one percent to one percent. Most of these differences in cover are small, and may be attributed to minor differences in growing conditions or to sampling error. *Hedysarum Mackenzii*, however, approximately doubled its cover from 1979 to 1980.

The *S. alaxensis* shrubs found in high gravel Stand B generally were less than 50 centimeters in height, but two percent of the shrubs were taller than 50 centimeters (Table 13). The range of ages determined by analyzing 25 ramets was 4-16 years with the mean occurring at 10 years (Figure 36).

The substrate for Stand B was largely gravel, 10-30 centimeters in diameter with an occasional rock to 40 centimeters in diameter (Tables 14 and 15). There were few fine particles.

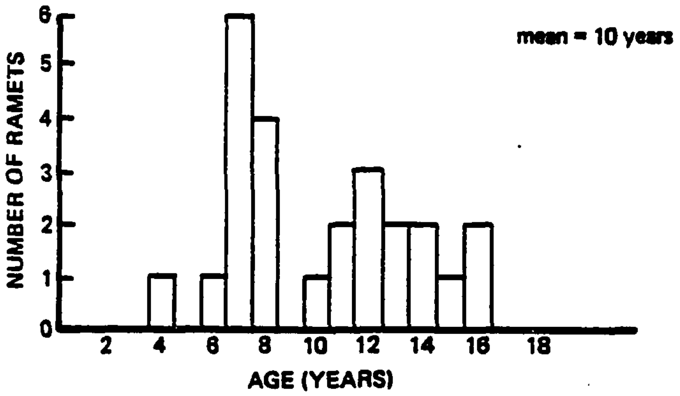

Figure 36. Age transect data from high gravel stand B, Happy Valley site. The sample consisted of 23 ramets collected from 25 genets.

Mature Stand D

The mature stand at Happy Valley appeared to be disturbed infrequently by flooding. Most disturbance probably occurred on the periphery. During periods of very high water or spring thaw, several low lying areas within the stand were filled with water (Figures 33 and 34). These intermittent ponds had a silt substrate and supported *Equisetum* and *Carex* species. In some instances the willows were larger and appeared more vigorous around the periphery of the ponds, a trait that was most apparent in the northwest corner of the stand.

Stand D was very large and contained considerable variation, making the sampling process difficult. The within stand variation included differing ratios of willow species, variation in height and vigor of S. *alaxensis*, variation in openness of the shrub layer and varying superficial soil moisture. Numerous differences in taxa composition and ground cover diversity occurred between mature Stand D and high gravel Stand B. Stand D contained 34 taxa compared to the 19 found in Stand B (Table 5a). Several of the additional taxa in Stand D seemed indicative of more moist and more poorly drained soils than those found in Stand B; such taxa were *Salix reticulata*, *Vaccinium uliginosum*, *Zygadenus elegans*, *Gentiana* spp., *Pinguicula* sp. and thallose liverwort. Three taxa which occurred in Stand B but not in Stand D were *Artemisia* spp., *Oxytropis Maydelliana*, and *Crepis nana*. Total cover for the Stand D was approximately 110 percent compared to the 34 percent for Stand B.

Collectively, taxa other than tall shrubs contributed the most cover in Stand D. The most important contributors in order of decreasing cover value were moss, *Arctostaphylos alpina*, *Hedysarum alpinum*, *Aster sibiricus*, grasses and *Senecio* spp. The remaining taxa contributed one percent or less to the total cover.

The tall shrub species, *S. alaxensis*, *S. hastata*, *S. glauca-brachycarpa*, *Shepherdia canadensis* and *S. lanata* contributed 25, 11, 9, 4 and less than one percent cover, respectively, to the stand. Species other than *S. alaxensis* were more important in mature Stand D than in high gravel Stand B.

Numerous taxa were found in 50 percent or more of the plots; in decreasing order of frequency, these taxa were moss, grasses, *Aster sibiricus*, *S. alaxensis*, *Senecio* spp., *S. glauca-brachycarpa*, *Arctostaphylos alpina*, *Hedysarum alpinum*, *S. hastata*, *Stellaria* sp., *Carex* spp., *Equisetum variegatum*, *Parnassia* spp., and *Gentiana* spp.

The *S. alaxensis* shrubs varied in vigor, height, age and amount of dead wood. Nearly two-thirds of the shrubs found in the plots exceeded .75 meter in height (Table 13). The age distribution for 24 ramets collected from approximately 15 genets ranged from 11 to 45 years. The mean age was 26 years (Figure 37). No *S. alaxensis* seedlings were observed in the plots but approximately 25 *Salix hastata* seedlings were found.

The substrate data from the plot sampling indicated that the substrate was 100 percent silt and sand (Tables 14 and 15). This substrate existed throughout most of the stand but there were few localized areas

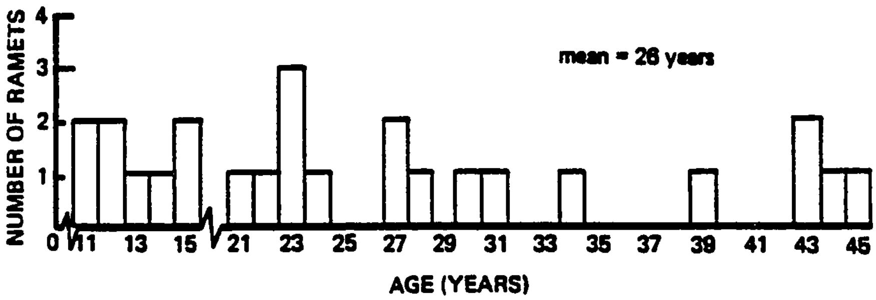

Figure 37. Age transect data from mature stand D, Happy Valley site. The sample consisted of 24 ramets collected from 15 genets.

of moderately sized gravel.

Other Stands

Numerous *S. alaxensis* communities existed at Happy Valley other than those previously described. One community was sampled quantitatively; others were qualitatively sampled. Many of the communities did not differ greatly from those quantitatively described; however, some differed substantially and are discussed below. Others are mentioned to clarify differences noted on the map (Figure 33).

Stand S

Stand S sampled at Happy Valley was not easily included in one of the four most common community types. The area was sampled because of interest in the high density of willow saplings. The stand was located in the silty portion of the gravel bar, east of and adjacent to the pond (Figure 33). It was a relatively small area similar in size to the low gravel Stand A. The stand did not appear to be severely disturbed during periods of high water; however, the water level of the pond fluctuated and probably was part of an overflow channel during very high water. During a moderately high water period, subterranean water was observed surfacing and flowing into the pond at its southern end. Near the end of summer during a very low water period, the pond dried completely. The water from the pond helped to keep the soil in Stand S very moist throughout most of the summer.

Stand S contained *S. alaxensis* saplings similar to those found in a high gravel stand. However, the stand differed from other young *S. alaxensis* stands in the high diversity of associated taxa, including taxa often found in mature stands, the high density of several species of willow and the silt and sand substrate.

Stand S contained 27 taxa compared with 34, 29 and 8 for the mature Stand D, high gravel Stand B and low gravel Stand A, respectively. These taxa provided 45 percent ground cover which was comparable to the 36 percent cover value found for high gravel Stand B (Table 5a). Those taxa contributing the most cover in Stand S were *S. alaxensis*, 10 percent; moss, 9 percent; grasses and *Equisetum variegatum*, 5 percent; and *Salix hastata*, *Equisetum* spp. and *Carex* spp., 2 percent each. All other taxa contributed one percent or less to the total cover. The taxa mentioned here were unusual for young colonization areas where gravel tended to be the primary substrate and where soil moisture appeared to be relatively lower. For example, in Stand B, *Epilobium latifolium* and *Hedysarum Mackenzii* were the two most important non-willow taxa.

In addition, Stand S contained more taxa in 50 percent or more of the plots than did high gravel Stand B (11 and 4, respectively). Three taxa, *S. alaxensis*, *S. hastata* and moss, were found in all plots in Stand S and two taxa, grasses and *Equisetum variegatum*, were found in all except one plot.

Several taxa were found in Stand S but not in Stand B (Table 5a). Many of these taxa, such as *Juncus* sp., *Eriophorum* sp., and *Carex* spp., are indicative of moist substrates. Some taxa found in Stand B but not in Stand S suggested that the substrate was drier in Stand B; these taxa were *Oxytropis campestris*, *Lupinus arcticus*, *Astragalus aboriginum*, *O. Maydelliana* and *Crepis nana*. The high soil moisture levels in Stand S may be important in maintaining the high density of willows.

In Stand S, *S. alaxensis* had a density of 13 saplings per square meter and *S. hastata* and *S. glauca-brachycarpa* had densities of 19 and 4 saplings per square meter, respectively. A total of 150 *Salix* seedlings were found in the plots. The ages of the *S. alaxensis* ramets based on 24 stems, ranged from three to nine years, with a mean of five years (Figure 38). Eighty-six percent of the *Salix alaxensis* saplings were less than .25 meter tall and the remaining were less than .50 meter tall (Table 13). One hundred percent and 99 percent, respectively, of the *S. hastata* and *S. glauca-brachycarpa* seedlings were less than .25 meter tall.

Stands P and R

Although mature Stand D contained considerable within stand variation, mature Stands P and R differed enough from Stand D to map separately (Figure 33). Stand P was a vigorous stand of tall *Salix alaxensis*, with few associated willows; the substrate had a greater percentage of large gravel than was generally found in mature stands. Stand R contained exceptionally tall *S. alaxensis* with some shrubs exceeding six meters in height. These were the tallest feltleaf

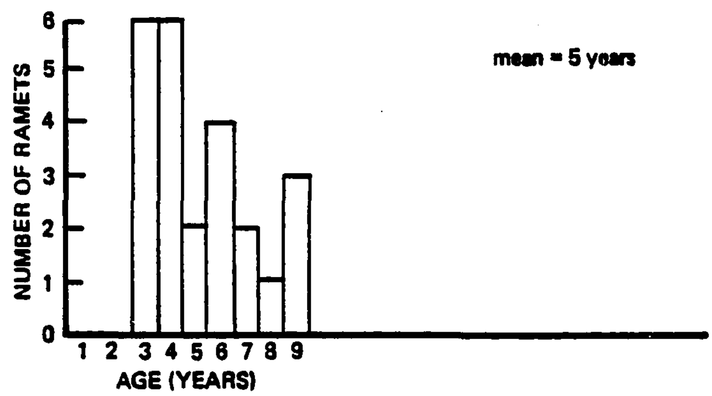

Figure 38. Age transect data from stand S, Happy Valley site. The sample consisted of 24 ramets collected from 24 genets.

willow seen along the Sag River drainage. Canopy cover was sufficiently dense to reduce herbaceous plants to a minimum; few taxa, mostly *Equisetum* spp., were seen. Stand R appeared to be flooded seasonally; the substrate surface was primarily silt.

Stand Q

Stand Q existed along the margins of a high water channel and contained scattered feltleaf willow of various ages, from seedlings to mature shrubs. The substrate also varied; gravel was predominant at the southern end and silt was predominant at the northern end of the stand. Associated taxa varied locally; the highest total cover was found on silt substrate at the northern third of the stand where *S. alaxensis*, *S. hastata*, *Equisetum* spp., sedges and rushes were the most important taxa.

Stands N and O

Like stand B, Stands N and O were high gravel stands; however, they differed in characteristics sufficiently to be mapped separately (Figure 33). Stand N contained *S. alaxensis* that were slightly larger and considerably denser than those found in Stand B; associated taxa and substrate traits did not differ substantially. In contrast, the occurrence of *S. alaxensis* in Stand O was very sparse and the shrubs assumed a more prostrate growth form than shrubs seen in other high gravel stands. Often sod clumps containing vegetation from mature or low willow communities were found in association with the shrubs.

The sod clumps were usually found to the side or downstream of the shrubs suggesting that a portion of feltleaf willow may have been deposited with the sod clump and produced a new shrub. Excavation of one of these shrubs gave no indication that it had originated from the sod clump, but rather from seed. If most of these shrubs originated from seed, then perhaps as the sod clumps were washed downstream, they caught on shrubs and the water forced the clump to the side or downstream without detaching it from the shrub.

Other Sites

Introduction

Sites sampled in 1979 but not in 1980 were 113-2, located in the northern Brooks Range along a mountain stream which was a tributary of the Atigun River; Oks Creek, Kuparuk River and Atigun River, tributaries of the Sag River; Flood Creek, a tributary of the Ivishak River which was also a tributary of the Sag River; and 120-2B, located along the Sag River (Figures 1a and 1b).

Stands representing the low gravel and high gravel community types were sampled at these sites; at 113-2 and 120-2B transition type stands were also sampled. Often stands were small and patchy and separated from other stands of the same community type by areas of barren substrate, stands of other community types or water.

In many stands of these sites, only slight differences were noted from stands of similar community types found along the Sag River (Tables 5a, 5b, 9a and 9b). Often these differences were due to species that rarely occurred in the community and to species which may have been left in a particular community after high water receded. Stands with characteristics differing from Sag River stands are mentioned in the following discussion.

Site 113-2

Site 113-2, located approximately 60 air kilometers south of the most southern Sag River site, 120-0, is the most southern and most mountainous site studied. Each of the sampled stands at 113-2 differed from Sag River stands in various ways. *Equisetum variegatum* and *Castilleja caudata*, common in the Sag River stands, were absent from all stands at 113-2. Although legumes were important in both the 113-2 and Sag River stands, *Astragalus* and *Oxytropis* spp. were more important at 113-2 and *Hedysarum* spp. were more important in the Sag River stands. The 113-2 low gravel stand contained nearly twice the number of taxa, including *S. glauca-brachycarpa* and *S. hastata*, of the Sag River stands. In the transition stand at 113-2, moss and lichens were more important than in transition stands from the Sag River.

Site 120-2B

Site 120-2B is located along the Sag River approximately 5 kilometers north of the intensive study site 120-0. Mining activities had left a large gravel area that had begun revegetating and resembled low gravel communities at other sites. Sampling of this low gravel area revealed no important vegetational differences from other low gravel communities. Other stands at this site resembled stands at other Sag River locations.

Oks Creek

Oks Creek is a meandering tundra stream with small point bars and little area for plant colonization. *Artemisia* spp. was an important taxon in the low and high gravel Oks Creek stands. In the low gravel stand, *Artemisia* spp. and *Epilobium latifolium* had higher cover values and were more widespread than *S. alaxensis*; in the high gravel stand, grasses, *Artemisia* spp. and *E. latifolium* were more important than *S. alaxensis*. In comparison to the Sag River low gravel stands, *E. latifolium* was slightly more important or of equal importance with *S. alaxensis* and in one high gravel stand, *Hedysarum Mackenzii* was nearly as important as *S. alaxensis*.

<u>Kuparuk River</u>

The Kuparuk River is primarily a tundra drainage system originating from a lake in the northern Brooks Range. Upper reaches of the river are meandering and lower sections are braided. Sampling occurred along a braided river section during a period of low water. The lack of fine soil particles and absence of several taxa, most legumes, *Aster sibiricus*, *Equisetum variegatum* and *Castellija caudata* were the most apparent broad differences between stands from the Kuparuk and the Sag Rivers.

The low gravel stand, located adjacent to standing water, contained a large number of taxa, including moss and *S. hastata*, and had high cover compared to Sag River low gravel stands. The stand more closely resembled the Sag River high gravel stands; the high water table probably contributed to these differences. In contrast, the Kuparuk River's high gravel stand contained fewer taxa and had lower cover than the low gravel stand; it resembled the least diverse Sag River high gravel stands which were found at site 120-0.

Flood Creek

Flood Creek is a clear, spring-fed stream on the northern edge of the Brooks Range. The sampling locations were immediately downstream from the transition of Flood Creek from a well-defined channel to a braided channel. Several taxa were absent from the Flood Creek stands that were common to Sag River stands; they include most legumes, *Aster sibiricus*, *Castilleja caudata* and *Senecio* spp. At Flood Creek the low gravel stand contained more taxa and had a higher total cover than the low gravel stands along the Sag River. *Salix hastata* and *S. lanata* were present at Flood Creek and absent from the low gravel stands along the Sag River; moss was also more important at Flood Creek.

Atigun River

The Atigun River is a glacial river originating in the Brooks Range. Sampling occurred at the mouth of the Atigun River. The largest *S. alaxensis* community was mature, but small areas of younger communities occurred along the river banks.

Several taxa commonly found in the Sag River low and high gravel stands that were absent from similar Atigun River stands were *Aster sibiricus*, *Castilleja caudata*, *Senecio* spp. and *Equisetum variegatum*. The other main difference between the sites occurred in comparison of the low gravel stands in which the Atigun River stand contained more taxa and had a higher total cover than the Sag River stands. *Epilobium latifolium*, *S. alaxensis*, and *Hedysarum Mackenzii* were the most important taxa in the low gravel stand at the Atigun River site.

POPULATION STUDIES

METHODS

Reproductive Potential 1979

In 1979, three study sites were selected for measurements of the reproductive potential of *Salix alaxensis*. They were mature stands adjacent to MS 113-1, MS 120-1 and MS 125-4. A 30 meter line transect was located in each area; cover by shrubs greater than 20 centimeters in height was recorded and percent cover was calculated. Shrubs crossed by the line were labelled and all catkins were counted on each shrub. Five percent of the catkins from each shrub were objectively collected for determination of numbers of capsules per catkin and seeds per capsule. In 1980, the sex of each shrub and the number of catkins per female shrub was recorded for each transect.

Reproductive Potential 1980

During the summer of 1980, a new method, designed to estimate seed production per unit area, was utilized to estimate reproductive potential. At the sites 120-0, 122-3, Happy Valley and 125-4, plots containing 25 to 30 complete shrubs were established in stands of the high gravel transition and mature community types.

The number of shrubs or genets encompassed by each plot was only an approximation since it was very difficult at times to determine what comprised an entire genet, e.g. one "shrub" at Happy Valley consisted of many male ramets and one female ramet. After excavating the ramets, the two were found to be of separate genets.

A complete shrub was defined as a shrub with all ramets originating within the plot boundaries. When this did not occur, i.e., some ramets occurred inside the plot and others occurred outside, the shrub was termed a partial shrub. A partial shrub was examined for male and female catkins; the absence of flowers was also noted.

Height of the tallest ramet of each complete and partial shrub was recorded. For each female complete and partial shrub, the number of catkins per ramet was recorded. If no catkins were present on a ramet that appeared to originate from a female shrub, that also was noted.

Later, when the catkins were at the early stages of dispersal, ten catkins were objectively collected from each plot and cover was estimated and recorded for all the *S. alaxensis* shrubs in the plot. The catkins were placed in plastic bags and frozen for later examination. When the catkins were thawed, their lengths were measured, the number of underdeveloped and developed capsules were counted, and ten developed capsules from each catkin were selected for seed counts. To count the seeds, each capsule was opened with a probe, and the fluff was carefully pulled out and examined for green seeds. The number of green seeds per capsule was recorded. In germination tests conducted on other seed lots, it is generally noted that 90 to 100 percent of the green seeds germinate.

Seed Rain

During the 1979 field season, seed traps were placed at three material sites. Four one-meter square ($1m^2$) frames filled with Jiffy Mix were placed at 114-1, 122-3, and 122-4. One plastic tray (31 x 24 centimeters), used as a water seed trap, was placed on one side of the Jiffy Mix trap. The Jiffy Mix traps measured numbers of germinating seed, whereas the water traps measured the amounts of seed rain. During dispersal the traps were visited every four to five days.

In 1979, 34 additional water seed traps were placed in undisturbed S. *alaxensis* communities adjacent to 114-1, 120-0 and Happy Valley runway. The traps were put in place prior to dispersal; distance between traps was 100 paces (i.e., .75 meter/pace or 75 meters).

During seed dispersal, the traps were examined every four days; seeds were counted and removed from the traps. Water was added periodically to maintain the level approximately one centimeter below the top of the tray.

Seedling Dynamics

Natural seedling establishment of *S. alaxensis* was observed throughout the summer of 1979 and in 1980 until July 6, at six permanent one-meter square plots. Two plots were located in the vicinity of each of the three material sites, 114-1, 120-2B and 125-4. Each plot was on a different soil type and had been left undisturbed by mining or construction activities. All plots were within 10 meters of a seed source.

Plot 1 at 114-1 was located on a gravel bar on the south bank of the main creek and north of Vanishing Creek. Plot 2 was north of the first one on a well-vegetated bank of the main creek. At 120-2B, plot 3 was established south of the access road in an overflow channel at the base of a cutbank; plot 4, north of the access road, was located on a silt and sand substrate near Seed Trap 5 (Figure 40). The fifth plot located at 125-4 was at the edge of the willow stand on a strip of silt and sand between the mature stand and mining area. The sixth plot was located on an old overflow channel near standing water. The substrate for this plot included medium size rocks in a matrix of silt and sand.

The plots were observed periodically for seedling survival and mortality with observations occurring more frequently during seed dispersal. Newly germinated seedlings were marked with toothpicks; toothpicks with seedlings no longer nearby were removed and the seedlings were counted as dead.

In addition to observing seedling establishment in permanent plots, general information was gathered on the percentage of fines and gravel found in areas of natural establishment of *S. alaxensis* seedlings.

At selected low gravel type sites, a square meter plot was established. The number of seedlings was counted and a standard shovel full of substrate was collected from the top 10 centimeters of soil. The sample was weighed, oven dried in accordance with procedures for gravimetric sampling and weighed again. After drying the sample was sieved using sieve sizes 37.5mm, 9.51mm, 2.38mm and .425mm. These sieve sizes do not represent divisions of particle sizes in standard soil classification systems, but were the only sieve sizes available in the field. According to the U. S. Department of Agriculture soil classification system, any particles exceeding 2mm in size are gravel. Particle sizes from .5mm to 2.0mm are coarse and very coarse sand, and particle sizes less than .5mm are finer grades of sand, silt and clay. The sieving process produced five particle size subsamples from each sample. The volume of each particle size was determined by the water displacement method.

RESULTS AND DISCUSSION

Reproductive Potential 1979-1980

The transects measuring reproductive potential in 1979 and 1980 revealed annual variations in flowering and catkin production. At 113-2 all shrubs produced more catkins in 1979 than they did in 1980. The percentage of shrubs producing catkins was also higher in 1979, 78 percent compared to 33 percent in 1980 (Table 16). All catkins that were counted on the transect in 1980 were poorly developed, i.e., there were few well-developed capsules. It is believed that cold weather at the time of pollination and early female catkin production was in part the cause of this poor development.

Little difference was noted in total catkin production at 120-1 between the two years; however, one shrub produced nearly two-thirds more catkins in 1980 than in 1979. Another shrub that had been a moderate producer in 1979 was also a moderate producer in 1980; this relationship also applied to low and high catkin-producing shrubs at 120-1. The percentage of catkin-producing shrubs on the transect differed slightly between the two years, being higher in 1979. One shrub that produced no catkins in 1979 produced one hermaphroditic catkin in 1980 (Table 16).

The third site, 125-4, produced one-third less catkins in 1980 than in 1979. Catkin production varied for each year on an individual shrub basis. However, more shrubs (67 percent) produced catkins in

Table 16. Number of catkins per *Salix alaxensis* shrub in 1979 and 1980[1]

	Site					
	113-2		120-1		125-4	
Shrub No.	1979	1980	1979	1980	1979	1980
1	9	2[2]	12	15	124	54
2	46	f	16	3	f	1
3	3	1	10	f	65	135
4	67	5[2]	?	1[3]	f	4
5	?	?	m	M	m	M
6	46	f	m	M	?	?
7	28	f	?	?	1	f
8	40	f	M	M	8	25
9	214	8[2]	150	237	?	?
10	?	?	11	9	489	130
11	?	?	17	1	38	65
12	26	f	10	4	230	250
13	88	3[2]	11	5		
14	26	f	9	2		
15	1	f	2	5		
16	?	?	f	2		
17	111	9[2]	2	f		
18	45	f				
Total No. of Catkins	750	28	250	285	955	664
Percent of shrubs producing catkins	78	33	65	59	58	67
F/M/?	14:0:4		12:3:2		9:1:2	
Sex Ratio	14:0:4	5:0:13	11:1:5	10:3:4	7:0:5	8:1:2
Percent of non-Flowering shrubs	22%		12%		22%	

[1] Symbols: f-no catkins, but sex of shrub female; ?-no flowers observed in either year, sex of shrub unknown; m-no flowers but sex of shrub male; M-flowers present, sex male.

[2] All catkins were poorly developed at 113-2 in 1980.

[3] Hermaphroditic catkin, sex considered unknown.

1980 than in 1979 (58 percent) (Table 16).

Considerable variation occurred between sites in the production of catkins per catkin-producing shrub, capsules per catkin and seeds per capsule. The value for one of these aspects of seed production might be relatively high within one stand while another might be low. For example, in 1979 at 125-4, a large number of catkins were produced per female shrub, but relatively few capsules per catkin and seeds per capsule were produced; at Happy Valley transition stand all values were relatively high (Tables 17 and 18). The variability could result from differences such as age, shrub vigor, genetics, and environmental condition, which could influence seed development at any stage.

The data presented in Table 18 show some general patterns of seed production. The transition stands were generally the most prolific seed producers (i.e., seeds/m^2), had the largest number of flowering shrubs per unit area and the highest number of catkins per square meter. The mature and high gravel stands were second and third, respectively, in seed production, number of flowering shrubs and number of catkins per square meter. An exception occurred at 125-4 where the mature stand was more productive in numerous respects and generally appeared to be more vigorous than the transition stand. The shrubs in the transition stand at 125-4 did not appear vigorous and the catkins contained only 50 percent developed capsules compared to 68 and 66 percent for the high gravel and mature stands, respectively, at 125-4.

Table 17. *Salix alaxensis* catkin and seed production in 1979

Site	Catkins per shrub, mean±SE	No. shrubs per transect	n-No. catkin-producing shrubs	Catkins per catkin-producing shrub, mean±SE	Developed capsules per catkin, overall mean[1]±SE	n[2]=total no. catkins collected	Seeds per capsule[3] mean±SE	Seeds per shrub	Catkin length, mm, overall mean±SE
MS 113-4	41.6±53.8	18	14	51.7±57.0	45.5±33.1	34	7.8±1.8	15,000	50.6±14.1
MS 120-1	14.7±35.4	17	11	22.7±42.5	75.9±26.1	16	5.4±1.7	6,000	61.3±14.2
MS125-4	79.6±146.8	12	6	136.4±174.6	44.8±28.7	47	4.5±2.1	16,000	63.3±22.9

[1]No significant differences between catkin-producing shrubs.

[2]5% of catkins per shrub sampled.

[3]Means for 5 capsules from one catkin per shrub.

[4]Determined by multiplying seeds per capsule x capsules per catkin x catkins per shrub.

Table 18. *Salix alaxensis* catkin and seed production in 1980

	Site											
	120-0			122-3			Happy Valley			125-4		
	High Gravel	Transition	Mature	High Gravel	Transition	Mature	High Gravel	Transition	Mature	High Gravel	Transition	Mature
Area (m^2)	28	314	123	79	113	71	23	43	75	12	55	69
% Cover (s.a.)	5	20	40	5	15	20	10	40	30	10	15	25
No. whole shrubs (genets)	32	31	26	30	34	31	26	29	31	31	28	31
No. partial shrubs[a]	1	11	5	0	6	5	1	3	7	0	3	1
Sex ratio (f/M/?)	2/0/30	22/7/2	8/1/4	1/1/28	14/4/1	11/2/18	6/0/20	18/9/2	14/12/5	1/0/30	11/2/15	18/6/7
No. female ramets/m^2[b]	.1	1.1	1.3	.03	1.8	.6	1.5	1.9	1.3	.2	1.5	1.4
Total No. of Catkins/m^2	.1	4.9	2.2	.01	4.1	1.1	.6	18.0	10.3	.1	5.5	5.6
Catkins/female ramets mean ± s.e.	.7±.4	4.6±.6	1.7±.4	.5±.5	2.2±.3	1.7±.6	.4±.20	4.4±.7	9.6±2.1	.5±.5	3.7±1.0	4.0±1.1
No. catkins collected	10	10	10	10	10	10	10	10	10	10	10	10
No. undeveloped capsules/catkins mean ± s.e.	100.7±13.9	171.7±9.8	178.1±5.3	109.8±14.6	125.8±14.6	105.2±20.1	39.0±6.8	52.9±12.4	83.7±12.2	50.5±9.7	82.9±7.6	53.7±13.6
No. developed capsules/catkins mean ± s.e.	60.7±12.3	40.3±9.7	34.7±7.4	61.2±15.8	73.3±16.0	79.6±22.3	128.4±10.6	137.0±20.8	91.7±17.5	109.4±12.3	82.0±15.3	104.0±16.7
Percent developed capsules/catkins	38	19	16	36	37	43	77	72	52	68	50	66
Catkin length (mm) mean ± s.e.	52.7±4.2	63.4±6.2	58.0±4.3	54.7±4.6	68.1±4.1	62.7±9.8	68.8±3.5	78.8±7.9	51.4±6.0	62.3±3.9	55.9±5.5	68.5±8.1
Total No. capsules counted for seeds	100	100	96[d]	100	100	81[c]	100	100	100	100	100	100
No. seeds/capsule mean ± s.e.	7.5±.4	7.7±.4	6.9±.4	7.6±.5	10.0±.4	10.1±.4	9.8±.5	11.2±.4	8.5±.4	6.8±.5	6.2±.5	8.1±.5
Estimate No. seeds/m^2[c]	35	1530	525	5	3025	825	765	27,655	9720	60	2810	4712
Shrub heights (m) all shrubs mean ± s.e.	.3±.02	1.1±.05	1.1±.05	.3±.02	.8±.05	1.0±.07	.3±.02	.7±.04	.7±.06	.2±.02	.5±.03	.9±.09

[a]Partial shrubs are included in counts of female ramets and total number of catkins, but not in number of whole shrubs.
[b]Includes partial shrubs.
[c]Total number of capsules counted was only 81 because one catkin had no developed capsules and another had only one developed capsule.
[d]Total number of capsules counted was only 96 because one catkin had only 6 developed capsules.
[e]Determined by multiplying seeds per capsule x capsules/catkins x catkin/female ramet divided by area of plot.

Although the high gravel stands were not producing as much seed per square meter as the other stands, percent developed capsules was equal to or higher than that of the mature or transition stands. The greatest difference occurred at 120-0 where the percent developed capsules from the high gravel stand was approximately two times greater than in the transition stands. No pattern emerged for the number of seeds per capsule (Table 18).

In terms of seed production, the high gravel stands produced 10-600 times fewer seeds per square meter than the other stands at each site. At three of the four sites, the transition stands produced approximately three times more seed per square meter than the mature stands. Under the conditions which influenced this seed crop, the two northern sites had the greatest overall seed production per square meter of feltleaf willow (Table 18).

Sex ratios of shrubs from the 1980 catkin and seed production plots differed from those of the shrubs from the 1979-1980 transects. The transects (placed in mature stands) had female to male ratios that varied from 4:1 to 14:0 (based on two years of data); non-flowering shrubs comprised between 12 and 22 percent of the population. Female to male sex ratios for the mature stands from the 1980 plots varied from 7:6 to 8:1 (based on one year of data); these ratios were within the range of the transect ratios. Female to male ratios recorded for the transition stands ranged from 2:1 to 5:1 and from 1:1 to 6:0 for the high gravel stands. The sex ratios for the shrubs from the high gravel stands are poor estimates of the true sex ratios because so few of the shrubs flowered. Non-flowering shrubs comprised between 16 and 58 percent of the shrubs of the mature stands; 6 and 54 percent of the transition stand shrubs and 77 and 97 percent of the high gravel stand shrubs. The transition stand at 125-4 had a large proportion of non-flowering shrubs compared to the other transition stands. Forty-seven shrubs were observed for flowering for two years. The results presented in Table 16 show that 21 shrubs had female flowers and one shrub had male flowers both years, 17 shrubs flowered only one year, seven shrubs did not flower either year and one shrub produced one hermaphroditic catkin. The variation in sex ratios and the occurrence of non-flowering shrubs could be related to numerous factors including age and environmental conditions.

The variation in sex ratios observed in stands of *S. alaxensis* might result from genetic based adaptive differences between males and females or from the alteration of the sexual expression of some individuals. The sex ratios of dioecious species have been shown to change markedly within short distances and have appeared to be correlated with changes in the environment, particularly with the availability of soil moisture. In several cases, male plants were found to have been less susceptible to moisture stress than female plants (Freemen, Klikoff and Harper 1976). If males are more successful than females in environmentally stressed conditions, then the species is likely to be successful in colonizing areas of patchy environmental conditions. Another explanation of different sex ratios might result from individuals changing their sex in response to environmental conditions, age, injury, disease or hormones. Studies have shown that numerous dioecious plants including several members of the Salicaceae have exhibited sex changes for these reasons. In these studies strong relations also existed for maleness in environmentally stressful conditions (Freemen, Harper and Charkov 1980; Freeman, Harper and Ostler 1980; and Freeman, Klikoff and Harper 1976).

Seed Rain

Willow seeds are small with fine cottony hairs and are easily dispersed by the wind. Seed dispersal can occur over long distances; however, the data from this study suggest that most seeds land near the seed source. Numerous studies on various species dependant on wind for dispersal of seed report similar findings, the bulk of the seed remains close to the parent plant and only small amounts of seed are dispersed long distances (Harper 1977).

The seed traps measuring dispersal for this study were in place for approximately thirteen days before the first seed count at 114-1, for twelve days at 120-2B and ten days at Happy Valley (Figures 39, 40 and 41).

Seed was dispersed earlier at 114-1 where 51 percent of the seed was dispersed by June 26 compared to 120-2B and Happy Valley where 16 and 25 percent of dispersal occurred by the same date, respectively. Seed dispersal was completed about the same time at all sites (Table 19).

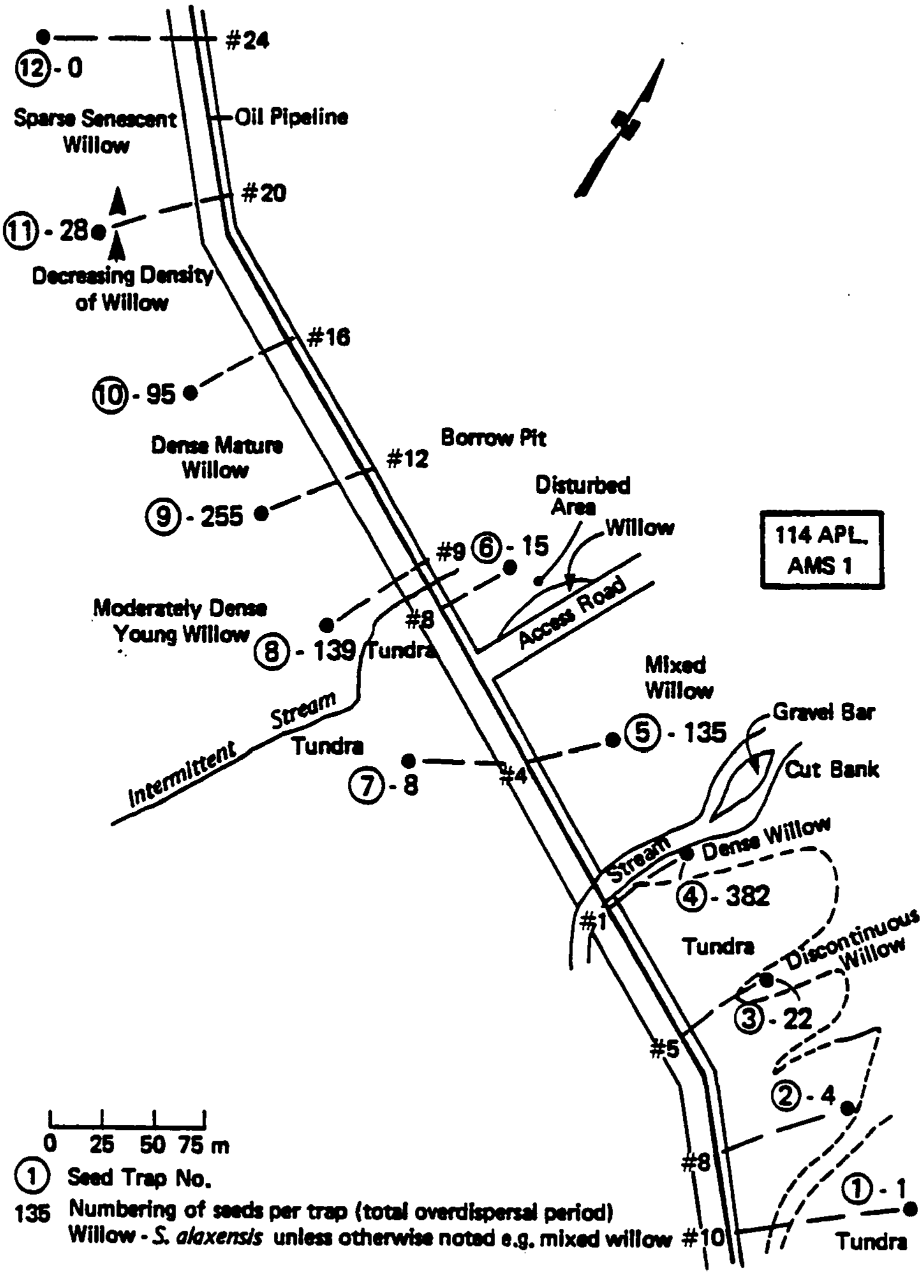

Figure 39. Map of seed traps at 114-1 (1979)

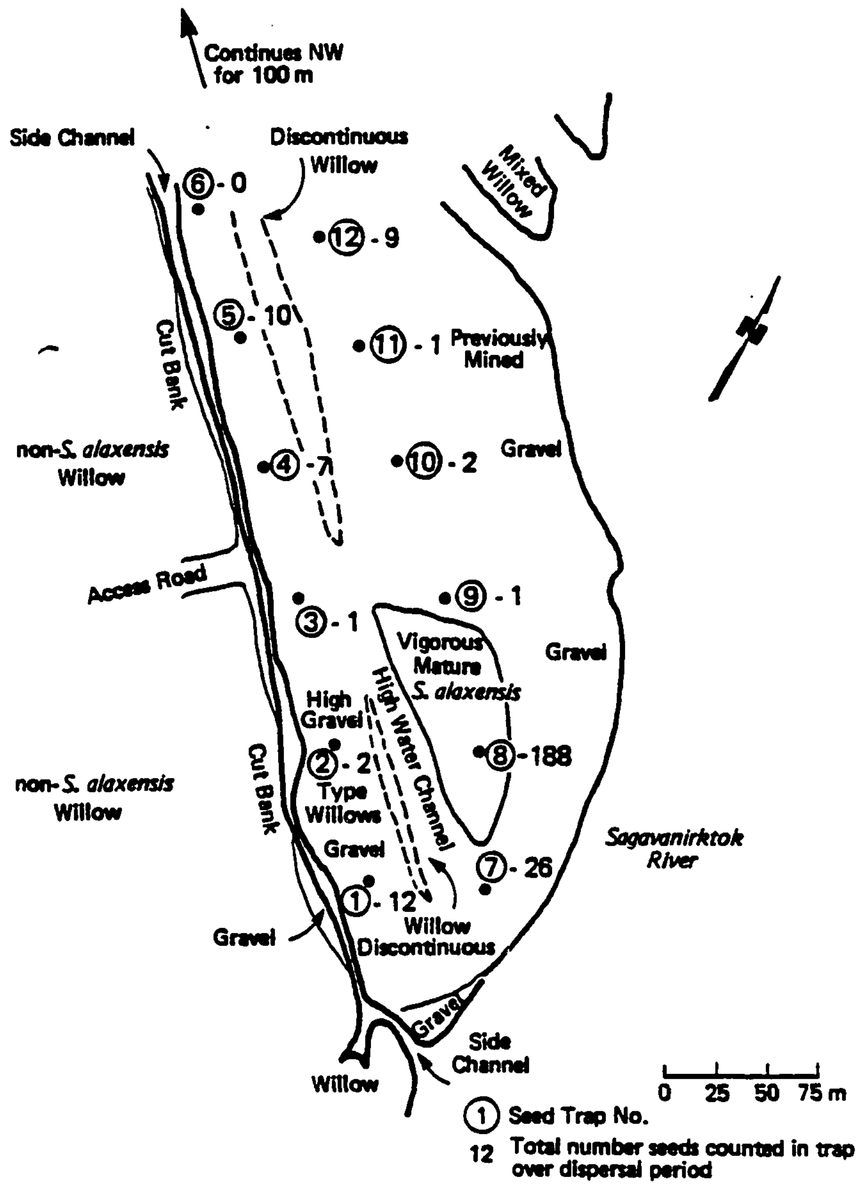

Figure 40. Map of seed traps at 120-2B (1979)

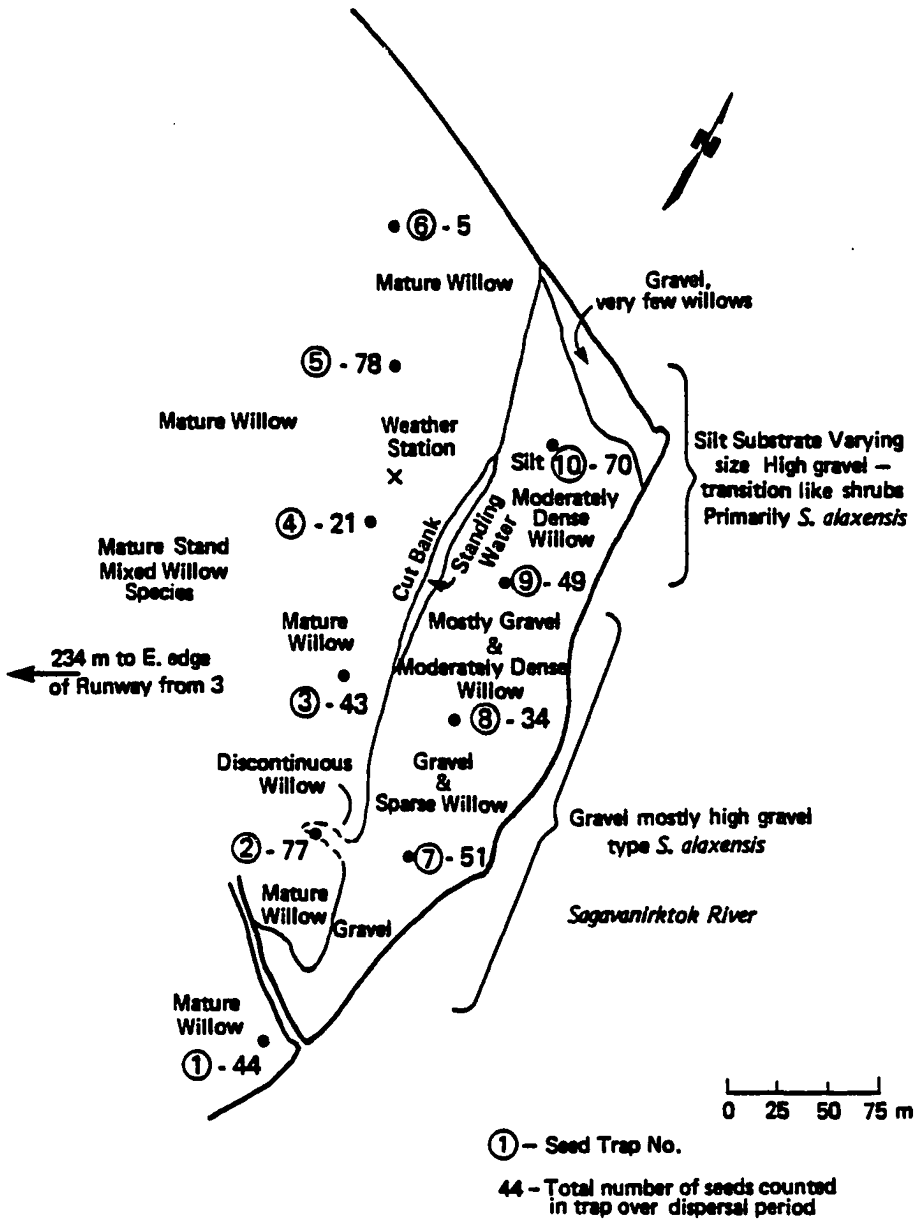

Figure 41. Map of seed traps at Happy Valley (1979)

Table 19. Number of *Salix alaxensis* seeds per square meter in undisturbed stands, 1979

	MS 114-1[1]					MS 120-2B[1]					Happy Valley[1]				
Trap No./Date	6/26	6/30	7/4	7/9	Σ	6/27	7/1	7/5[4]	7/9	Σ	6/27	7/1	7/5	7/10[6]	Σ
1	0	9	0	0	9	19	93		0	112	47	121	168	75	411
2	9	19	9	0	37	0	9		9	18	168	224	317	9	718
3	103	65	19	19	206	0[5]	9		0	9	84	121	168	28	401
4	1939	1044	494	84	3,561	0[5]	65		0	65	28	28	112	28	196
5	820[2]	317	103	19	1,259	9	56		28	93	298	401	19	9	727
6	28	65	37	9	139	0[5]	0		0	0	0	0	37	9	46
7	28	9	37	0	74	56	149		37	242	56	196	224	0	476
8	569	624	103	0	1,296	149	475		196	820	112	196	9	0	317
9	997	1016	308	56	2,377	0	0		9	9	121	103	214	19	457
10	569	308	9[3]	0	886	0	19		0	19	168	363	121	0	652
11	56	84	103	19	262	0	9		0	9					
12	0	0	0	0	0	9	37		37	83					
Percent	51	35	12	2	100	16	62		22	100	25	40	31	4	100
Σ	5118	3560	1222	206	10,106	242	921		316	1479	1082	1753	1389	177	4401

Note: Actual number of seeds collected per seed trap can be found by dividing number in table by 9.3.

[1] Dates traps were set out – 114-1: 13 June 79; 120-2B: 15 June 79; Happy Valley: 17 June 79.

[2] The trap is located about 1.5 m west of a shrub loaded with catkins – yet this is the highest count for the seed trap. A possible explanation for this low count is that the prevailing winds are from the north and south.

[3] Trap move, probably kicked over by moose.

[4] Material site was under water, traps were not evaluated.

[5] Traps are full of sand and silt probably a result of hard rains and the sand splashing into traps. Seeds could have splashed out of traps.

[6] *Salix hastata* has begun to disperse and are found in the traps; sometimes in large numbers. They appear to be much smaller than *S. alaxensis* seeds, and were differentiated on that basis.

Although most individual seed traps appeared to have the same dispersal pattern as the general pattern for the stand, some differed. For example, trap 11 at 114-1 received 21, 32 and 39 percent of its seed on June 26, 30 and July 4, respectively, but the stand's general dispersal pattern was 51, 35 and 12 percent for the same observation dates. Because the life of willow seeds is short (Densmore 1980), timing of dispersal is important in determining which microsites have seedlings.

Differences in total seed rain were also noted between sites. The highest seed rain occurred at 114-1, followed by Happy Valley and 120-2B. The amount of seed reaching each trap was highly variable at 114-1 particularly when compared to the relatively uniform distribution of seed at Happy Valley (Table 19).

Several factors affected the number of seeds found in individual traps; they include proximity to a seed source, amount of seed produced by the shrubs, wind patterns during dispersal and weather. Wet weather causes the cotton hairs to become matted and lose their bouyancy. The traps that collected the most seed were close to a good seed source, e.g. trap 4 at 114-1 (Figures 39, 40 and 41).

Seedling Dynamics

The pattern of germination and establishment of feltleaf willow was observed on six square meter plots; each plot had a different substrate and was subject to different environmental conditions. Feltleaf willow germinated on plots with moist substrates. Establishment was most successful when the substrate remained moist most of the summer, physical disturbance was minimal and competing vegetation was sparse.

Plot 1 on the gravel bar near 114-1 was characterized by a surface of 50 percent rocks with silt and sand in between. Thirty-five percent of the rock surface was composed of rocks greater than 20 centimeters in diameter. The silt and sand surface was predominantly moist throughout most of the season. At the time the plot was established in early July 1979, the peak of seed dispersal had passed but small amounts of seed continued to be dispersed through mid-July.

In 1979, Plot 1 was inundated twice causing seedling deaths from burial or erosion. In most cases, burial probably accounted for the highest mortality. The toothpicks marking the seedlings may have contributed significantly to burial since they often caught debris and then became a focal point for deposition of sand and silt. By the end of the 1979 summer, two seedlings and four *S. alaxensis* saplings, two to four years old, were alive. The six willows survived the winter and the floods from spring thaw and were found in the plots in early summer 1980.

Plot 2 was not subject to the flooding of Plot 1. This plot showed high summer survival in 1979, but high mortality occurred during the winter (Table 20). The plant cover of Plot 2 was approximately 60 percent with a wide diversity of taxa; in decreasing order of percent cover, the taxa were: *Carex* sp., *Hedysarum alpinum*, *S. alaxensis*, *Polygonum viviparum*, grasses, mosses, lichens, *Parnassia* sp.,

Table 20. Natural seedling establishment

	MS 114-1					MS 120-2B					MS 125-4			
	Plot 1		Plot 2			Plot 3		Plot 4			Plot 5		Plot 6	
Date	Alive[1]	Dead[2]	Alive	Dead	Date	Alive	Dead	Alive	Dead	Date	Alive	Dead	Alive	Dead
1979														
7/4	389	0	375	0	7/1&3	114	0	104	0	6/29	148	0	50	0
7/9	301[1,3]	162[3]	456	0	7/9	129[3]	15[3]	110	14	7/5	60	107	184	6
7/26	237	105	– No Data –		7/22	117	18	109	4	7/12	21	59	211	1
8/25	2[3,4]	235	409	47	8/23	56[3]	61[3]	48[3]	61[3]	7/22	1	20	210	1
										8/26	1	0	177	33
1980														
6/21	6[5]	0	19	390		–	–	–	–	6/23	0	0	75	102
6/29	10	0	20	0	6/26	129	35	9	48	7/3	0	0	194	0
7/6	34[3]	4	35	0	7/6	132	39	247	0	7/6	6	0	297	3

[1] This figure represents total alive seedlings (new and previously counted seedlings).

[2] Numbers in the dead column indicate the number of seedlings that died since the last visit to the plot.

[3] Plots have been inundated since last visit.

[4] In addition to the 2, 1979 seedlings, there are 4 saplings established in previous years in plot.

[5] Includes the 4 saplings.

Aster sibiricus, *Pedicularis* sp., and *S. arctica*. The remaining 40 percent of surface was mineral soil which occurred primarily on the southern side of the plot. Germination occurred most frequently on the mineral surfaces although some did occur on moss. Seedlings occurred in dense clusters and they remained very small with one to three true leaves. The leaf size also remained very small, and some seedlings appeared etiolated.

In 1980, Plots 1 and 2 had few *S. alaxensis* germinants. Numerous factors could have contributed to low germination; however, the most likely factors were low seed production and dispersal in the area.

The plots at 120-2B exhibited little difference in seedling survival in 1979 from those at the other sites, despite the differences in substrate. Plot 3 had 85 percent rock cover, 40 percent of which was rocks 20-40 centimeters in diameter. The rocks were covered with a fine layer of glacial silt. The plot was located on the edge of an overflow channel of the Sag River at the base of a cutbank. Seedling survival was reasonably good despite two floods (Table 20). The channel was not subject to swift water during summer flooding and although the water was quite silty, the plot was not in an area subject to heavy silt and sand deposition or erosion like that which occurred in Plot 1.

The substrate of Plot 4 was entirely sand and silt, the surface of which remained moist most of the summer. The plot was in the flood plain of the Sag River and near a small intermittent stream which helped to keep the plot moist except during prolonged dry spells when the surface would dry out. This plot was inundated during the summer;

a portion of the plot was eroded while sand was deposited on another part. At this time the highest seedling mortality occurred. No seedlings survived the winter and spring floods at 120-2B; overwinter seedling survival was lowest at 120-2B probably because of the heavy spring flooding that occurred along the Sag River. In 1980, more seedlings were counted on the plots at 120-2B than in 1979, particularly on Plot 4; in contrast, fewer seedlings were counted on the plots at 114-1 in 1980 than 1979 (Table 20).

The plots at 125-4 were very different from each other. Plot 5 had no rocks on the surface, but consisted of silt and sand of fine particle size. The surface dried quickly, exhibiting a caked, cracked and powdery surface. Although germination occurred in the plot in 1979, seedlings persisted the longest in the deep cracks where moisture was retained longer and the seedlings were protected from the high soil surface temperatures. In 1980, although fluff associated with seed dispersal was observed on all soil surfaces, only six seeds were observed to have germinated in the deep cracks. The warm weather and lack of rain in this area during seed dispersal probably accounts for the low seedling count (Appendix B). Although Plot 5 was close to seed-producing willows, it was far from the river or any standing water. It appeared to be dependent on rainfall (or extreme high water) to keep it moist. Therefore, the seedlings died quickly when soil surfaces dried and cracked.

Plot 6 was located in what appeared to be an old overflow channel. Considerable colonization by willow was occurring nearby.

The plot surface was characterized by 30 percent rock less than 20 centimeters in diameter with sand and silt in between. The finer soil material had pulled away from the rock providing numerous protected areas for successful germination and seedling establishment. A pool of standing water was within five meters of the plot. The level did not fluctuate much until the end of the summer when it receded noticeably. The presence of this water might be indicative of a high water level which kept the surrounding soils moist and contributed significantly to the success of seedling establishment in this plot. (Observations in early summer 1980 indicate that much of the water comes from snow melt from a large snow drift.) The surface of this plot was moist when Plot 5 was dry and cracked. Only at the end of the summer when the water level dropped did more seedling mortality occur. This plot did not appear to be flooded during spring or summer high water periods.

Seventy-five seedlings survived the winter in Plot 6, ten of these appeared to be older than one year (Table 20). Minimal disturbance and favorable environmental conditions probably were very important to the high survival. The data for 1980 appear to follow a pattern similar to that of 1979; the number of seedlings observed in the plot was comparable for both years.

Successful establishment of *S. alaxensis* seedlings appeared to depend upon the seeds falling on a moist, sparsely vegetated, mineral substrate that remained moist most of the summer. Competition from other plants appeared to reduce seedling vigor, as seen in Plot 2, and minimize successful seedling establishment. Plots 1, 3 and 4 were moist most of the summer but were also flooded periodically. Summer flooding caused some seedling mortality by burial or erosion, but flooding associated with spring thaw probably caused the highest mortality of seedlings that had become established during the summer. The most successful seedling establishment plot, number 6, was moist most of the summer, had a gravel, silt and sand substrate, was sparsely vegetated, and did not appear to have been disturbed by moving water.

The possible relationship between particle size and successful seedling establishment can be examined in Table 21. The percentage of fines found in areas of seedling establishment generally was low. The Kuparuk River No. 1 and 113-2 sites had the lowest percentage, 4 percent, for particle sizes less than .425mm. The Kuparuk site supported a very high number of saplings and seedlings. The site was moist when most areas of equivalent height above surface water were dry. The presence of surface moisture appeared to be a critical factor for germination and seedling establishment particularly in soils of low water-retaining capacity.

These data do not yield conclusive evidence on a relationship between percent fines and seedling establishment; however, they do suggest that factors (e.g. moisture availability and depth to water table) other than the presence of fines are more important to seedling establishment.

Table 21. Percentage of gravel, coarse sand, and fines in microsites where *S. alaxensis* seedlings are establishing, and number of saplings and seedlings.

	Particle Size (%)						
	--- Gravel (mm) ---			Coarse Sand	Fines	No. of	No. of
Location	>37.5	>9.51	>2.38	>.425mm	>.425mm	Saplings	Seedlings
Flood Creek No. 6	26	49	9	9	7	20	6
Kuparuk No. 1	24	40	17	15	4	97	100+
Flood Creek No. 5	41	38	5	7	9	8	0
Kuparuk No. 3	46	37	Trace	5	11	9	0
Kuparuk No. 2	36	41	10	9	5	5	5
Flood Creek No. 4	37	49	Trace	2	12	8	0
MS 113-2	22	39	16	19	4	12	5

SUMMARY AND CONCLUSIONS

Two main conclusions regarding vegetational and species dynamics emerge from the study of *Salix alaxensis* dominated vegetation along the Sag River and adjacent drainages: 1) a general pattern of succession seems to exist which is related to allogenic, primarily fluvial, factors and autogenic factors; and 2) variation in structure, composition and fluvial processes are evident in stands of the approximate same general successional stage.

The general successional pattern suggested below is developed from comparisons of different stands and sites over a two year period not from following specific sites for long periods of time. This type of evidence may lead to serious error, but the patterns presented below are general and probably reasonably accurate.

In brief, the postulated successional pattern involves first the colonization of newly emerged river alluvium by feltleaf willow and herbaceous plants. As the river moves away from the newly colonized area, *S. alaxensis* shrubs grow larger, produce seed and develop more complex branching patterns; other species of willow invade the area, herbaceous taxa become more diverse, finer soil particles accumulate, the vegetative mat becomes thicker and soil temperatures decrease. This gradual process of successional change apparently may occur uninterrupted from the seedling establishment phase until senescence or may be interrupted at any stage by the effects of flooding of the

Sag River (Stand L at 120-0).

Riparian vegetation, such as feltleaf willow communities and fluvial processes are closely intertwined exerting influence on each others' pattern of development. The powerful spring floods carrying rocks, ice and other debris scour channels (Stand Q at 120-0) and abrade vegetation (Stand L at 120-0). Vegetation helps to stabilize river banks and modifies the movement of water. As a result, silt and sand often settle out on the downstream sides of the willows burying branches which then root adventitiously and send up new shoots; thus the river stimulates vegetative spread of the shrubs. Fluctuations in the level of the river that occur after spring thaw are important in determining the availability of a seedbed and the success of seedling establishment.

Salix alaxensis colonizes newly emerged river alluvium along the Sag River simultaneously with herbs. This is in contrast to reports by Gill (1971) that *S. alaxensis* follows *Equisetum fluvatile* in succession on the Mackenzie River Delta. The substrate on the Mackenzie Delta is silty and *S. alaxensis* possibly needs the stabilizing influences of *E. fluvatile* for successful establishment. In the study areas along the Sag River, the substrate was very gravelly with few fine soil particles. As long as these gravelly soils remained moist throughout most of the summer, *S. alaxensis* was able to become established in the 'safe sites' (Harper 1977) which occurred between the gravel particles. Adequate protection from flood waters for the young germinants and saplings also must have been provided by the gravel substrate. The time frame for such establishment is unknown. It may be that many years and many "false starts" are required before environmental conditions allow the successful establishment and continued growth of the earliest pioneer communities.

Establishment of the *S. alaxensis* plants that dominate the low gravel communities along the Sag River appears to occur chiefly by seed; newly germinated seedlings were observed in the stands. This is in contrast to Bliss and Cantlon (1957) who stated that along the Colville River the earliest feltleaf willow shrubs originated from material deposited on the gravel bar. Portions of larger feltleaf willows have washed up and rooted on the Sag River gravel bars and it is conceivable that small sapling-sized feltleaf willows could also be deposited and become established in these areas. Newly emerged alluvium could be colonized by larger portions of feltleaf willow being washed in and becoming established. However, in this situation the shrubs would be larger than those in areas where colonization occurs by seed or young saplings. Establishment of *S. alaxensis* by sod may occur more frequently further downstream.

Timing is also an important factor in the successful establishment of a young feltleaf willow community. Seed dispersal must coincide with the availability of safe sites and a seed source must be relatively nearby in order to ensure adequate seed rain. Feltleaf willow produces abundant seed, the bulk of which falls near the parent plant; some seed is dispersed long distances by air and/or water and is capable of reaching sites removed from the seed source.

Those areas with favorable conditions and near a seed source probably are capable of producing dense stands of *S. alaxensis* saplings, e.g. Stand Y at 120-0.

Seeds dispersed by water may be deposited and become established in a line defining a high water level (Stands O and T at 120-0). Shrubs established by vegetative means could also form such a line.

As the *S. alaxensis* saplings grow, they become more complex structurally and often develop several basal branches. At approximately the ages of 6-10 years, the shrubs begin to flower. Associated vegetation in these stands is generally more diverse than in younger stands and legumes, particularly *Hedysarum Mackenzii* may be sufficiently well developed to be codominant with *S. alaxensis*.

Complexity continues to increase as the shrubs mature; many shrubs become multiple stemmed as basal branches are buried during floods. These mature shrubs, approximately 15-20 years old, are generally at least .75 meter in height with one to several ramets and little or no dead wood. They are usually heavy seed producers. Flowering of both male and female shrubs seems to peak during this vigorous mature stage of shrub growth, which is characteristic of many transition stands, and to decline as mature shrubs become senescent. The specific ages of flowering, peak seed production and amount of seed produced varies genetically and with environmental conditions including annual variations in weather.

The most vigorous shrubs and the most prolific seed-producing shrubs generally occurred in areas where the herbaceous and low shrub strata were not well developed and most of the mineral substrate was exposed. These areas appeared to be flooded periodically, which suggests that some disturbance helps to maintain vigor in *S. alaxensis* communities.

Salix alaxensis is the dominant shrub for the communities studied along the Sag River for approximately 50 years. However, usually by this time other willows, namely *S. glauca-brachycarpa*, *S. hastata* and *S. lanata*, which are more tolerant of the cooler, more poorly drained soils, have invaded the communities. Willows continue to play a dominant role in riparian succession for many years in the arctic compared to the subarctic where willows may remain in a stand but are quickly replaced by poplar and spruce as the dominant plants (Johnson, Viereck, et. al. 1966; Johnson and Vogel 1966; and Viereck 1977).

The successional stage beyond the senescent mature *S. alaxensis* community along the Sag River presumably varies according to site, but often consists of shrub vegetation dominated by *S. glauca-brachycarpa*, *S. hastata* and some *S. lanata* with a variety of herbs and mosses forming a dense ground cover (Stand C at 120-0). This stage perhaps is similar in appearance to the first terrace community described by Bliss and Cantlon (1957) for successional communities along the Colville River; however, it differs in composition. The terrace community contains alder as the dominant shrub and the willows, *S. planifolia* and *S. arbusculoides*. Alder was absent from the communities on the Sag River floodplain.

Variability occurs among the stands of any one community type and among sites but no obvious patterned arrays could be detected. The number of combinations of variables determining the specific vegetation of these early successional stands undoubtedly is very high. The number of stands of each type that could be sampled may have been too low to detect patterns or there may not be enough stands of the possible variants to detect patterns by sampling. The early successional communities, particularly the high and low gravel stands, are very unstable, sparsely vegetated and influenced by many allogenic factors, including fluvial processes, substrate composition and conditions, proximity to seed source, other physical factors, and chance. As vegetation becomes more consolidated and mature, as in some transition stands and the mature stands, gradient arrays and/or subtype separation might be expected to become apparent. This study concentrated on early stages and very few mature consolidated stands were included.

In spite of the lack of detectable consistent patterns, several variants within the types warrant discussion. Several early successional communities, i.e., low gravel and high gravel stands, contained S. *glauca-brachycarpa* and/or S. *hastata*. These stands included the high gravel Stands Q and W at 120-0, the low gravel stands at 122-3 and the Kuparuk River, and the low and high gravel stands at 120-2B and Oks Creek. These species were found only in the later successional stages at the remaining sites. Legumes were very important at the 120-0 and 113-2 sites and nearly absent from the Flood Creek site; variations in substrate, chance and availability of a seed source may help to explain these differences. Oks Creek is the only site where *Artemisia* sp. was a major component of the herbaceous flora. Characteristics of the shrubs also differed between stands; e.g. the shrubs in the transition Stand C at 122-3 were generally shorter and wider than the shrubs from other transition stands. The degree of fluvial disturbance also differs with each stand; the stands at 120-0 provide good examples of variation due to this factor.

Despite the differences that occur, some uniformity exists in these pioneer communities. Although the amount varies, three taxa, *S. alaxensis*, *Epilobium latifolium* and grasses are present in nearly all stands and *Hedysarum Mackenzii* occurs in many low and high gravel stands but was absent in stands with more well-developed vegetation. The remaining taxa varies with stand and site.

Additional sampling and mapping may yield more detailed information on these pioneer communities. Further investigations would benefit from an interdisciplinary approach, with more emphasis placed on the geomorphology of fluvial interactions with plant succession and population characteristics.

APPENDICES

APPENDIX A

Population characteristics and branching patterns

of *Salix alaxensis* ramets by community type

Table A-1. 120-0 Site: High Gravel Stand W

Age	Dry Weight (g)	Basal Diameter (cm)	Height (cm)	Length of Longest Current Growth (cm)	Total Non-Dehiscent Branches	No. Non-Dehiscent Branches/Order Order of Branching 1	2	3	4	5	6	Total Non-Dehiscent Branches	No. of Dehiscent Branches/Order Order of Branching 1	2	3	4	5	6
2	.14	.30	12	8	1	1						1	1					
3	.08	.25	3	2	0	no branches – stem all zero order						0						
4	.28	.31	12	8	1	1						3	2	1				
4	.46	.47	15	11	2	1	1					4	3	1				
4	2.58	.72	25	7	2	2						9	2	7				
4	3.68	.35	8	10	3	3						0						
7	.90	.42	21	3	1	1						4	2	2				
7	10.73	.99	56	15	8	6	2					7	3	3	1			
8	.92	.52	12	4	1	1						2	2					
8	1.95	.55	18	12	8	6	2					6	1	4	1			
8	2.69	.45	26	26	2	2						2		2				
9	4.19	.95	29	7	11	4	6	1				7		6	1			
9	8.65	.77	45	7	11	5	6					22	4	10	8			
9	13.39	.95	48	10	9	7	2					32	3	24	5			
10	1.56	.64	19	6	4	4						4	2	2				
10	2.94	.75	23	4	8	3	5					15	2	4	9			
10	11.50	1.22	36	6	16	3	9	4				45		13	26	6		
10	15.69	1.20	47	7	21	6	9	4	2			43	4	13	20	6		
10	19.96	1.70	41	9	21	3	7	11				38		11	16	11		
11	1.15	.76	14	8	4	4						5	1.	4				
11	9.34	1.40	35	10	18	7	10	1				16	1	8	7			
11	12.13	1.38	36	15	18	10	8					23	3	9	11			
11	14.77	1.61	53	19	12	7	3	2				20	4	8	6	2		
11	16.43	1.19	48	13	16	4	9	3				26		9	16	1		
12	7.27	.85	36	12	20	3	6	6	3	2		25	5		10	2	8	
				Total	218	94	85	32	5	2		359	45	141	137	28	8	
				Percent of Total	100	43	39	15	2	1		100	13	39	38	8	2	

Table A-2. 120-0 Site: High Gravel Stand Q

Age	Dry Weight (g)	Basal Diameter (cm)	Height (cm)	Length of Longest Current Growth (cm)	Total Non-Dehiscent Branches	No. Non-Dehiscent Branches/Order Order of Branching 1	2	3	4	5	6	Total Non-Dehiscent Branches	No. of Dehiscent Branches/Order Order of Branching 1	2	3	4	5	6
1	.46	.29	21	21	0		no branches – all zero order					0						
3	.06	.12	11	9	0		no branches – all zero order					0						
3	.83	.36	20	7	3	2	1					1	1					
3	1.70	.53	21	15	2	2						5	3	2				
3	5.79	.90	34	21	10	6	4					9	4	5				
4	3.54	.58	40	20	4	3	1					1	1					
4	5.24	.66	34	42	5	2	3					6	6					
5	2.30	.56	31	16	5	4	1					4	2	2				
5	3.31	.68	50	47	3	2	1					1	1					
5	3.59	.70	30	20	4	2	2					1	1					
5	7.82	.83	39	23	7	5	2					15	3	12				
5	14.67	.96	41	16	20	6	11	3				42	4	17	17	4		
6	11.11	.93	50	15	22	8	10	4				32	3	9	19	1		
6	26.48	1.10	80	52	12	12						4	4					
8	5.06	.74	44	6	8	3	3	2				12	4	6	2			
8	18.30	1.06	68	48	14	6	7	1				10	1	8	1			
8	37.92	1.18	73	19	13	4	4	4	1			27		11	10	6		
9	55.98	1.58	73	22	56	9	20	26	1			471	1	11	25	4		
10	47.06	1.77	51	15	56	16	31	8	1			117		39	63	15		
11	41.00	1.95	57	13	40	5	14	15	6			38		3	12	22	1	
12	67.79	1.71	74	12	54	9	26	17	2			71	3	19	25	23	1	
				Total	338	106	141	80	11			437	42	144	174	85	2	
				Percent of Total	100	31	42	24	3			100	9	33	39	19	< 1	

Table A-3. 120-0 Site: Transition Stand J

Age	Dry Weight (g)	Basal Diameter (cm)	Height (cm)	Length of Longest Current Growth (cm)	Total Non-Dehiscent Branches	No. Non-Dehiscent Branches/Order Order of Branching 1	2	3	4	5	6	Total Non-Dehiscent Branches	No. of Dehiscent Branches/Order Order of Branching 1	2	3	4	5	6
6	.87	.95	40	6	4	1	3					1			1			
7	10.40	.60	32	4		no branches – zero order stem						2	2					
8	2.02	.82	62	4	6	4	2					7	1	4	2			
11	8.83	.81	–	–	–	–	–	–	–	–	–	–						
11	102.88	2.63	100	10	24	4	8	12				35		4	13	18		
12	11.96	1.34	89	14	4	3	1					8	3	5				
12	42.63	2.06	74	9	23	5	13	5				27		10	16	1		
13	11.61	1.12	64	5	8	6	2					11	3	6	2			
13	38.97	1.81	80	7	10	6	4					19	2	13	4			
14	45.98	1.42	87	15	4	2	2					8	1	4	3			
15	38.22	1.00	75	9	17	8	8	1				17	2	5	10			
17	36.70	2.36	62	10	15	3	6	6				21		10	8	3		
17	105.98	2.54	89	12	23	7	8	5	3			34	1	6	21	3	3	
18	138.84	2.73	134	11	54	9	24	17	4			50		13	23	12	2	
19	57.53	2.01	72	24	22	3	10	9				28		6	12	10		
19	73.12	1.91	85	11	39	3	12	19	5			47		3	20	24		
19	81.51	1.91	94	15	33	5	13	9	6			38	1	6	15	8	8	
20	48.02	1.69	100	6	18	1	3	9	5			14			2	9	3	
20	91.57	2.19	90	18	18	6	6	6				12		2	5	5		
21	44.70	1.66	89	19	13	3	6	4				18		4	6	8		
21	96.93	2.37	105	15	12	6	4	2				19	1	11	5	2		
23	79.95	2.93	89	10	22	8	11	3				11		3	8			
23	244.40	3.35	198	32	67	6	26	19	14	1	1	113		40	14	39	18	2
24	94.23	2.10	111	13	24	5	7	6	5	1		26	1	4	7	10	4	
25	117.04	2.27	103	12	26	8	14	4				39	1	10	22	6		
				Total	486	112	193	136	42	2	1	605	19	169	219	158	38	2
				Percent of Total	100	23	40	28	9	< 1	< 1	100	3	28	36	26	7	< 1

Table A-4. 120-0 Site: Transition Stand M

Age	Dry Weight (g)	Basal Diameter (cm)	Height (cm)	Length of Longest Current Growth (cm)	Total Non-Dehiscent Branches	No. Non-Dehiscent Branches/Order Order of Branching						Total Non-Dehiscent Branches	No. of Dehiscent Branches/Order Order of Branching						
						1	2	3	4	5	6		1	2	3	4	5	6	7
3	1.29	.89	32	26	1	1						3	3						
6	12.08	.78	73	15	9	4	3	2				10	3	3	2	2			
7	17.45	1.04	66	11	13	2	6	5				10	1	1	5	3			
9	29.01	1.01	57	8	39	6	11	15	7			25		1	6	14	4		
9	42.12	1.45	87	21	29	4	8	16	1			13		4	4	5			
9	92.00	2.55	95	11	32	5	15	9	3			22		4	12	6			
10	32.04	1.59	93	11	14	2	6	4	2			21		5	7	8	1		
11	23.90	1.49	64	15	13	3	6	4				18		3	8	7			
11	28.30	1.04	95	9	34	8	7	8	9	2		29		7	5	10	7		
11	88.73	2.15	145	15	30	3	14	9	4			53	1	4	25	15	8		
12	107.91	2.13	109	22	35	6	16	10	3			29		4	15	10			
13	48.80	1.78	84	10	9	1	2	4	2			4		3	1				
15	61.78	1.55	84	17	42	7	10	14	7	4		41		10	14	15	2		
15	63.82	1.80	90	10	23	8	14	1				15		8	7				
15	79.68	1.72	97	36	39	6	11	14	7	1		42	1	5	15	18	3		
15	226.15	3.03	142	30	100	16	58	25	1			42		11	28	3			
16	91.69	2.57	120	6	19	1	6	8	4			15		2	4	6	3		
18	286.06	3.13	173	27	27	9	18					51	3	23	25				
18	347.12	2.84	164	25	79	10	33	24	11	1		54		9	19	20	6		
19	40.50	1.87	59	10	56	5	20	21	7	3		26		3	13	9	1		
19	126.09	2.92	130	24	68	2	11	24	27	4		45		1	10	20	14		
20	107.56	2.83	122	8	35	8	12	12	2	1		45		13	14	16	2		
20	170.74	2.57	100	25	58	3	12	25	13	5		14			7	3	4		
21	268.78	3.88	121	24	135	3	20	54	47	11		124			22	56	42	4	
28	578.92	3.36	136	29	225	7	43	83	66	23	3	125		3	39	37	38	6	2
				Total	1164	130	362	391	223	55	3	876	12	127	307	283	135	10	2
				Percent of Total	100	11	31	34	19	5	< 1	100	1	15	35	32	16	1	< 1

Table A-5. 120-0 Site: Mature Stand F

Age	Dry Weight (g)	Basal Diameter (cm)	Height (cm)	Length of Longest Current Growth (cm)	Total Non-Dehiscent Branches	No. Non-Dehiscent Branches/Order Order of Branching 1	2	3	4	5	6	Total Non-Dehiscent Branches	No. of Dehiscent Branches/Order Order of Branching 1	2	3	4	5	6
10	29.17	1.88	81	12	13	1	7	4	1			10		3	7			
10	41.00	1.68	88	27	20	4	8	6	2			27	1	6	13	7		
14	35.08	1.92	95	26	8	1	3	4				10		1	4	5		
16	38.06	1.90	73	16	21	3	10	8				18		1	11	6		
17	104.05	2.45	117	34	39	4	20	15				42	1	7	21	13		
17	132.21	2.27	95	27	33	4	14	11	4			21		1	11	8	1	
18	43.91	2.13	90	19	3	1	1	1				4		1	2	1		
18	70.28	1.75	93	34	15	3	7	4	1			17		3	10	4		
18	162.05	2.85	135	33	52	5	10	13	15	9		45	2	2	12	11	18	
19	103.53	1.96	94	20	38	3	14	17	4			38		6	14	18		
19	111.47	3.29	100	45	39	5	17	15	2			49		11	20	18		
21	221.00	3.65	122	24	78	13	24	26	15			94	1	19	33	24	17	
22	115.35	2.47	66	16	49	7	22	14	4	2		47		12	27	5	3	
22	118.60	2.36	108	28	25	9	11	3	2			30	1	21	7	1		
24	74.14	2.88	121	47	18	1	3	7	4			8			1	6	1	
24	90.44	2.25	85	32	19	1	3	8	5	2		20		1	1	15	3	
28	135.14	2.53	106	36	27	1	8	9	5	4		57			1	15	21	20
30	250.23	4.21	134	32	42	3	4	14	12	8	1	63		1	6	22	26	8
31	125.74	2.32	121	30	9	2	7					11		7	4			
31	390.38	3.63	150	56	65	9	23	25	6	2		69	1	8	23	30	7	
31	419.72	4.00	186	32	67	3	17	23	18	5	1	68		2	20	20	24	2
32	287.75	3.11	146	20	56	10	26	19	1			48	1	11	28	8		
33	223.80	3.50	165	34	40	2	6	13	18	1		43			9	24	10	
34	164.12	3.54	120	37	60	10	15	21	14			45	1	4	15	23	2	
35	104.13	2.30	121	21	11	2	1	2	5	1		12				1	11	
				Total	847	107	281	282	138	37	2	896	9	129	314	291	143	10
				Percent of Total	100	13	33	33	16	5	< 1	100	1	14	35	33	16	1

Table A-6. 120-0 Site: Stand L

Age	Dry Weight (g)	Basal Diameter (cm)	Height (cm)	Length of Longest Current Growth (cm)	Total Non-Dehiscent Branches	No. Non-Dehiscent Branches/Order Order of Branching						Total Non-Dehiscent Branches	No. of Dehiscent Branches/Order Order of Branching					
						1	2	3	4	5	6		1	2	3	4	5	6
2	2.53	.56	45	40	2	2						0						
8	10.97	1.10	46	9	7	5	2					16	3	8	5			
8	22.33	1.04	51	8	15	7	8					15	2	3	10			
9	19.51	1.32	55	39	6	6						12	2	10				
9	25.56	1.27	72	28	25	10	12	3				8	1	4	3			
11	38.76	1.83	69	14	21	7	8	4	2			18		3	9	6		
12	10.81	.91	49	13	6	5	1					10		8	2			
12	49.76	1.54	117	41	24	7	11	6				26		10	13	3		
13	27.17	1.85	60	25	12	2	4	6				10		4	3	3		
13	67.31	2.08	61	11	40	8	14	10	8			63	2	9	31	15	6	
14	10.79	1.00	34	18	12	7	4	1				16		7	9			
14	22.70	1.42	58	4	5	2	3					4		3	1			
15	77.49	2.03	76	19	37	7	18	10	2			18		8	8	2		
15	81.42	1.91	113	45	35	7	19	8	1			16		6	8	1	1	
15	132.09	2.11	108	38	56	15	12	14	14	1		61	4	18	23	8	8	
15	282.67	3.58	175	95	68	21	24	19	4			72	1	20	32	13	6	
18	128.99	3.73	100	27	37	6	16	11	4			21		5	7	6	3	
22	227.68	2.88	52	11	13	6	4	3				9		4	5			
25	364.93	3.57	137	46	71	4	11	27	20	9		57		5	12	21	17	2
32	537.34	3.12	151	22	133	31	28	46	28			132	2	16	44	53	17	
35	529.63	5.72	123	10	44	13	22	6	2	1		42	1	11	24	3	2	1
42	715.79	5.05	150	49	133	24	49	37	19	4		73	4	17	23	21	8	
47	482.62	4.98	210	43	82	12	25	26	13	4	2	50			24	16	6	4
50	100.26	4.37	65	25	42	10	16	11	5			24		2	16	6		
				Total	926	224	311	248	122	19	2	773	22	181	312	177	74	7
				Percent of Total	100	24	34	27	13	2	< 1	100	3	23	40	23	10	1

Table A-7. 122-3 Site

High Gravel Stand B			High Gravel Stand H		
Age	Dry Weight (g)	Basal Diameter (cm)	Age	Dry Weight (g)	Basal Diameter (cm)
1	.09	.23	3	.05	.26
3	.28	.29	3	.83	.37
3	.50	.34	4	.08	.21
4	.02	.18	5	.14	.25
4	.11	.19	5	.55	.42
4	.14	.29	5	.64	.32
4	.27	.28	5	1.38	.43
4	.35	.23	6	.46	.31
4	.70	.35	6	1.10	.47
4	1.38	.42	7	.55	.36
5	.90	.51	7	.83	.41
6	.10	.25	7	1.20	.41
6	1.10	.46	7	1.20	.43
6	1.30	.56	7	1.49	.58
6	6.40	.77	8	.55	.34
6	6.70	.84	8	.60	.41
7	1.60	.62	9	5.80	.79
8	2.70	.73	9	6.51	1.23
8	7.00	.83	10	.92	.46
11	7.90	.95	10	1.56	.40
12	17.20	1.23	10	1.66	.52
13	39.50	1.50	10	3.68	.54
14	56.60	1.72	11	2.71	.83
			12	5.24	.85

Table A-8. 122-3 Site

Transition Stand C			Mature Stand E		
Age	Dry Weight (g)	Basal Diameter (cm)	Age	Dry Weight (g)	Basal Diameter (cm)
3	.51	.29	13	63.72	3.69
4	.63	.34	14	43.53	1.76
5	2.42	.59	15	25.48	1.36
6	1.47	.48	16	53.20	2.50
6	6.67	.81	16	175.77	2.67
7	7.59	.75	17	187.24	3.88
7	10.90	.78	18	25.74	2.20
7	14.58	1.00	19	181.70	2.73
8	4.63	.84	19	270.76	3.13
8	10.99	.90	19	410.00	3.64
8	11.95	1.05	20	30.85	2.72
8	24.57	1.18	20	225.47	2.73
10	16.06	1.11	21	55.44	1.75
11	22.08	1.20	22	783.07	4.33
11	55.98	1.58	23	721.07	4.15
11	97.82	1.82	27	164.57	2.43
12	21.37	1.44	27	408.82	3.10
12	61.13	1.28	28	517.39	4.23
14	18.18	1.13	30	72.62	2.21
14	137.24	2.15	30	220.08	2.70
15	84.78	1.80	32	30.65	2.87
16	58.97	1.85	32	115.56	3.84
17	70.01	1.86	34	96.55	4.16
18	100.49	2.47	34	385.92	4.31
			37	526.21	4.12

Table A-9. Happy Valley Site

Low Gravel Stand A			Stand S		
Age	Dry Weight (g)	Basal Diameter (cm)	Age	Dry Weight (g)	Basal Diameter (cm)
1	.005	.10	3	.09	.18
1	.006	.07	3	.18	.25
1	.014	.11	3	.46	.32
1	.017	.07	3	.55	.35
1	.017	.11	3	1.66	.70
1	.020	.13	3	2.30	.52
1	.023	.11	4	.18	.25
1	.026	.18	4	.74	.43
1	.029	.13	4	.83	.41
2	.005	.06	4	.86	.54
2	.005	.07	4	4.69	.68
2	.007	.10	4	5.70	.69
2	.029	.18	5	.55	.36
2	.030	.14	5	.92	.45
2	.063	.15	6	.28	.31
2	.080	.23	6	.46	.38
2	.080	.25	6	.64	.45
2	.081	.32	6	2.21	.52
3	.061	.18	7	.46	.38
3	.079	.18	7	1.30	.45
4	.040	.16	8	.50	.61
7	.074	.25	9	2.02	.68
			9	7.91	.83

Table A-10. Happy Valley Site

Mature Stand D			High Gravel Stand B		
Age	Dry Weight (g)	Basal Diameter (cm)	Age	Dry Weight (g)	Basal Diameter (cm)
11	154.99	2.17	4	1.21	.37
11	266.99	2.37	6	1.56	.58
12	3.75	.67	7	.55	.36
12	85.96	2.04	7	3.76	.74
13	56.69	1.80	7	4.74	.69
14	57.15	1.23	7	5.15	.72
15	10.69	1.34	7	7.13	.75
15	48.28	2.83	7	7.18	.52
21	94.69	2.17	8	.74	.38
22	90.29	3.14	8	1.10	.43
23	30.25	1.49	8	1.29	.39
23	87.40	1.82	8	8.28	.82
23	100.31	2.15	10	6.27	.72
24	321.37	3.59	11	5.89	1.04
27	59.80	3.04	11	9.43	.94
27	147.34	2.96	12	4.88	.73
28	154.99	2.45	12	13.99	1.21
30	583.92	4.30	12	18.34	1.07
31	42.21	1.65	13	7.5	.90
34	235.94	3.13	13	17.85	1.35
39	1254.16	4.79	14	6.74	1.23
43	119.09	3.66	14	9.48	.96
43	516.92	4.61	15	8.09	1.17
45	1057.21	3.63	16	14.19	1.07
			16	42.83	1.81

APPENDIX B

Environmental Data

ENVIRONMENTAL DATA METHODS

Environmental data were collected as part of the large scale research project on willow revegetation. The data presented here apply specifically to naturally established stands.

In 1979 and 1980 air and soil temperatures were recorded throughout the growing season utilizing Grant recorders. Recordings were replicated and thermistors were placed at 1m and 5cm above the ground level and at soil depths of 2.5, 10, 20 and 50cm. Measurements were made in establishing, transition (at one site only) and mature *Salix alaxensis* communities at MS 113-2, Oks Creek, MS 122-3 and Happy Valley. Temperatures were recorded for MS 122-3 in 1979 only; in 1980, the recorder and probes from MS 122-3 were used to replace damaged equipment at other sites.

Precipitation was measured at weekly intervals from single standard rain gauges places at MS 114-1, Oks Creek, MS 122-3 and Happy Valley in 1979; in 1980 measurements were also made at MS 113-2.

Table B-1. Air and soil temperatures in natural stands during 1979 growing season (°C)

	Air										Soil															
	1m					5cm					-2.5cm					-10cm					-50cm					
	Absol		Mean		Mnthly	Absol		Mean		Mnthly	Absol		Mean		Mnthly	Absol		Mean		Mnthly	Absol		Mean		Mnthly	
Site & Month	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Date[1]
Mature Stands																										
May																										
Oks Ck	19	-6	10	2	5	28	-6	15	7	-1	11	1	7	2	4	4	1	3	2	2	–	–	–	–	–	(21-31)
MS 122-3	16	-6	9	-2	3	19	-5	11	-2	4	11	0	7	1	4	7	0	4	1	3	–	–	–	–	–	(20-31)
June																										
Oks Ck	24	-2	16	3	10	35	-1	23	2	11	14	2	11	5	8	9	2	6	4	5	–	–	–	–	–	
MS 122-3	25	-2	15	3	10	28	-1	18	3	11	17	3	13	6	10	13	4	11	7	8	12	4	9	7	8[2]	(no 6/11)
Happy Valley	23	-7	15	1	8	25	-6	17	2	9	16	-2	11	6	8	16	-2	9	5	7	15	-6	5	3	4	(14-30)
MS 113-2	–	–	–	–	–	24	1	16	5	10	15	4	12	6	9	10	3	9	5	7	5	2	4	3	3	(21-30)
July																										
Oks Ck	28	-1	20	5	13	34	1	25	5	14	19	6	14	9	11	14	6	11	9	10	–	–	–	–	–	(1-21)
MS 122-3	26	1	20	7	13	30	2	22	7	14	19	6	16	10	13	16	7	14	11	12	15	7	13	11	12	
Happy Valley	29	1	21	8	15	30	3	22	9	16	21	8	18	13	15	19	9	16	13	15	17	8	13	12	13	(4-31)
MS 113-2	–	–	–	–	–	28	2	21	7	13	18	5	14	8	11	14	4	11	8	9	10	3	6	5	6	
August																										
Oks Ck	27	0	16	5	11	19	4	15	9	12	24	-3	16	5	10	16	8	14	11	12	–	–	–	–	–	(16-31)
MS 122-3	24	4	20	7	14	26	5	21	8	12	18	8	16	11	13	15	9	14	11	13	13	9	12	10	12	(1-15end)
Happy Valley	24	-3	18	5	12	27	1	18	7	12	22	7	15	12	14	20	8	15	12	14	17	10	14	13	13	
MS 113-2	–	–	–	–	–	26	4	17	7	11	17	3	12	8	10	13	4	11	8	9	9	5	8	7	7	(no 8/8)
September																										
Oks Ck	19	-8	8	-2	3	13	0	7	3	3	18	-7	7	-2	2	11	3	[illegible]	5	6	–	–	–	–	–	(1-22)
MS 122-3, no data																										
Happy Valley	15	-4	9	-1	4	20	-1	11	1	5	11	5	9	6	8	10	6	9	7	8	10	8	9	9	9	(1-10)
MS 113-2	–	–	–	–	–	22	-5	5	-1	1	10	-1	5	2	3	8	0	5	3	4	6	1	4	3	4	(1-20)
Low-High Gravel Stands																										
May																										
Oks Ck	17	-6	9	-1	4	21	-4	13	0	6	21	1	10	3	8	16	2	10	4	7	–	–	–	–	–	(21-31)
MS 122-3	17	-6	9	-2	3	17	-5	10	-1	4	18	0	12	1	6	14	0	9	2	5	–	–	–	–	–	(20-31)
June																										
Oks Ck	23	-2	15	3	9	35	0	20	5	12	29	4	21	9	15	24	5	18	10	14	–	–	–	–	–	
MS 122-3	24	-2	15	3	9	26	0	17	4	11	25	3	19	7	13	21	4	16	8	12	7	3	6	5	5	(no 6/11)
Happy Valley	22	-7	13	2	8	22	-5	15	3	9	21	-1	16	6	11	17	-1	12	7	9	15	-3	7	5	6	(14-30)
MS 113-2	21	1	14	4	9	26	2	15	5	10	27	4	18	8	13	21	4	15	8	12	10	5	9	7	8	(21-30)
July																										
Oks Ck	27	0	19	6	13	36	3	29	8	18	32	6	25	12	18	27	8	21	13	17	–	–	–	–	–	(1-21)
MS122-3	26	1	19	7	14	29	2	22	8	15	29	4	23	11	17	26	7	20	12	16	10	5	9	8	8	
Happy Valley	29	1	21	8	15	29	3	22	10	17	27	6	22	12	17	22	7	18	13	16	16	7	13	12	12	(4-31)
MS 113-2	26	1	18	7	3	28	2	20	8	14	29	4	22	10	15	28	5	19	11	15	14	6	12	10	10	
August																										
Oks Ck	23	-5	15	4	10	23	-1	16	7	11	16	7	14	11	12	21	0	14	7	11	–	–	–	–	–	(16-31)
MS122-3	26	4	20	8	14	25	6	21	9	14	25	8	20	11	15	23	9	19	11	15	11	8	10	10	10	(1-15 end)
Happy Valley	24	-3	17	6	12	26	0	18	7	13	27	4	19	10	14	23	6	16	12	14	17	9	14	13	13	
MS 113-2	24	3	16	7	11	24	1	17	7	12	27	2	17	8	12	19	4	15	9	12	12	5	10	8	9	(no 8/8)
September																										
Oks Ck	17	-8	6	-2	2	16	-4	7	0	3	11	2	6	4	5	12	-4	5	0	3	–	–	–	–	–	(1-22)
MS 122-3 no data																										
Happy Valley	16	-4	9	-1	4	18	-2	11	0	5	13	2	11	4	7	11	4	9	6	7	8	7	9	8	9	(1-10)
MS 113-2	– out –					14	-7	6	0	2	16	-3	7	1	3	12	-1	6	2	4	9	-1	5	2	3	(1-20)

[1] Dates temperature recorded, if not for full month.

[2] -50cm measurements began 12 June.

Continued on next page.

Table B-1. continued

	Transition Stand																									
	Air										Soil															
	1m					5cm					-2.5cm					-10cm					-50cm					
	Absol		Mean		Mnthly	Absol		Mean		Mnthly	Absol		Mean		Mnthly	Absol		Mean		Mnthly	Absol		Mean		Mnthly	
Site & Month	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Date*
June MS 113-2	24	1	14	4	9	26	2	16	5	10	16	7	13	9	11	14	7	12	9	11	9	6	9	7	8	(21-30)
July MS 113-2	26	1	19	7	13	29	2	21	8	14	19	7	16	11	13	17	7	15	11	12	14	7	11	10	10	
August MS113-2	24	0	16	6	11	25	1	18	7	12	17	5	14	10	12	16	6	12	10	11	13	7	11	9	9	(no 8/8)
September MS 133-2	17	-10	6	-2	1	16	-7	7	-1	2	10	-1	5	2	4	9	0	5	3	4	8	2	5	4	5	(1-20)

*Dates temperature recorded, if not for full month.

Table B-2. Air and soil temperatures in natural stands during 1980 growing season (°C).

	Air										Soil															
	1m					5cm					-2.5cm					-10cm					-50cm					
	Absol		Mean		Mnthly	Absol		Mean		Mnthly	Absol		Mean		Mnthly	Absol		Mean		Mnthly	Absol		Mean		Mnthly	
Site & Month	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Max	Min	Max	Min	Mean	Date[1]
A. Mature Stand																										
June																										
Oks Crk	24	1	17	6	12	32	1	23	6	13	15	2	11	6	8	10	2	7	5	6	4	0	2	1	2	6-12; 27-30
Happy Valley	25	-3	17	5	12	28	-2	20	5	13	17	0	12	7	9	14	0	9	6	8	8	-2	4	3	3	7-17; 19-30
MS 113.2	24	-1	13	4	8	26	0	15	4	9	14	0	9	4	7	11	0	6	4	5	5	-1	2	1	1	10-30[2]
July																										
Oks Crk	26	-2	16	4	10	35	1	19	5	11	19	7	15	11	13	15	9	13	11	12	14	5	12	11	11	3-31
Happy Valley	29	-1	15	4	10	28	0	19	5	11	18	5	13	9	11	15	5	12	9	10	10	6	9	8	8	1-31
MS 113.2	21	-2	18	6	10	25	0	18	6	11	16	3	13	8	10	13	4	11	8	9	11	4	7	6	7	3-31
August																										
Oks Crk	25	-4	13	1	6	35	-4	16	1	7	18	3	11	7	9	14	5	10	9	10	15	7	10	9	10	1-31
Happy Valley	23	-5	11	1	6	22	-4	12	3	6	16	4	10	7	8	14	5	9	7	8	11	6	9	8	8	1-31
MS 113.2	21	-5	11	1	6	26	-4	19	1	7	14	1	12	4	6	11	2	7	5	6	7	1	5	4	4	1-31
September																										
Happy Valley	3	-7	0	7	-4	2	-4	1	-3	-1	4	2	4	3	3	5	3	4	4	4	7	5	6	5	6	1-3
MS 113.2	1	-9	-2	-7	-4	4	-8	1	-6	-2	2	0	1	2	1	3	1	2	1	1	4	2	3	2	2	1-5
B. Regenerating Stand																										
June																										
Oks Crk	22	1	16	7	12	33	2	20	8	14	31	3	22	10	16	25	5	18	11	15	18	7	14	12	10	
Happy Valley	23	-2	16	5	11	26	-2	18	6	12	24	1	17	8	12	20	2	14	8	11	11	0	6	5	6	
MS 113.2	19	-3	12	1	7	20	-1	14	3	8	24	1	17	4	10	19	1	13	5	9	10	1	6	4	5	
July																										
Oks Crk	23	-3	14	4	10	26	-1	18	7	12	26	2	20	9	14	22	4	17	11	14	19	6	14	12	13	
Happy Valley	27	-1	14	4	9	29	0	16	6	11	26	3	17	9	13	21	5	13	10	12	11	6	9	8	8	
MS 113-2	22	4	15	8	12	23	-1	15	7	11	25	0	18	8	13	21	2	16	10	12	14	4	11	9	10	
August																										
Oks Crk	26	-5	12	1	6	22	-1	12	2	7	23	0	13	5	8	19	1	11	6	8	13	4	9	7	8	
Happy Valley	21	-6	11	2	6	23	-4	12	3	7	21	1	13	6	9	17	3	11	7	8	11	6	9	8	8	
MS 113-2	14	4	8	6	7	21	-4	11	1	6	21	-2	13	3	10	18	1	12	4	8	13	2	9	5	7	
September																										
Happy Valley	2	-7	-2	-6	-4	2	-5	1	-3	-1	3	1	2	1	2	3	2	3	2	3	6	5	6	5	5	
MS 113-2	4	-4	3	1	3	2	-9	-1	-6	-4	1	-5	0	-3	-2	1	-1	1	0	1	3	0	2	1	1	
C. Transition Stand at MS 113.2																										
June			(no data)				23	-2	15	2	8	17	0	12	5	8	15	2	11	7	9		(no data)			
July							24	-1	16	7	10	17	4	14	10	12	16	5	13	10	12	13	5	11	10	10
August							22	-4	12	2	6	15	1	10	5	7	13	3	9	6	7	13	3	8	6	7
September							3	-7	1	-3	-1	2	1	2	1	1	4	1	2	1	1	4	1	3	2	2

[1]*Dates temperature recorded if not for full month. Dates of record apply to all stand types at each site.*

[2]Single replicate per sample.

Table B-3. Monthly total precipitation during 1979-1980 growing seasons
Expressed as cm of water, 1978-80

Site	Month					Summer	Start	Stop
	May	June	July	August	Sept.	Total	Date	Date
1979								
MS 114-1[a]	–	2.49	5.00	8.86	.74	17.09	7 June	21 Sept.
Oks Creek	3.05[b]	6.17	6.96	10.87	–	24.00	19 May	15 Sept.
MS 122-3	2.72[b]	5.36	6.88	7.65	.97	20.85	19 May	15 Sept.
Happy Valley	–	4.29	5.92	7.04	1.22	18.47	12 June	21 Sept.
1980								
MS 113-2	–	4.01	8.99	5.74	1.04	19.79	9 June	7 Sept.
MS 114-1	–	4.32	9.30	5.54	.79	19.94	9 June	7 Sept.
Oks Creek	–	6.86	12.90	7.75	–	27.51	6 June	27 Aug.
MS 122-3	–	2.84	8.56	9.17	2.36	22.94	7 June	3 Sept.
Happy Valley	–	3.99	5.03	7.82	2.39	19.23	6 June	3 Sept.

[a]Data are included because it was near MS 113-2.

[b]Excluded from total.

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